THE EMBRYOLOGY OF SOME SOLANACEAE

ABSTRACT

THESIS SUBMITTED FOR THE AWARD OF THE DEGREE OF

Doctor of Philosophy

IN

BOTANY

FAIQ AHMAD KHAN

DEPARTMENT OF BOTANY
ALIGARH MUSLIM UNIVERSITY
ALIGARH

1983

ABSTRACT

The morphology and embryology of *S. aethiopicum* L., *S. citrullifolium* A.Br., *S. integrifolium* Lam., *S. khasianum* Clarke and *S. sisymbrifolium* Lam. have been described.

1- The habit, external morphology and floral characters of the above mentioned species have been described.

2- Differentiation of floral parts takes place in acropetal succession.

3- The flowers are pentamerous and actinomorphic in *S. aethiopicum*, *S. integrifolium*, *S. khasianum* and *S. sisymbrifolium*, while pentamerous and zygomorphic in *S. citrullifolium*. Occasionally the flowers may be tetramerous and hexamerous in *S. sisymbrifolium*, hexa and heptamerous in *S. aethiopicum* and *S. integrifolium*. The calyx is persistent and gamosepalous in all the five species. The calyx is accrescent in *S. citrullifolium* and *S. sisymbrifolium*. The corolla is gamopetalous, and campanulate in *S. aethiopicum*, *S. integrifolium*, *S. khasianum* and *S. sisymbrifolium*. However, the corolla is zygomorphic in *S. citrullifolium*. Anthers are bithecous and 4-chambered. Heteroanthy is a usual feature in *S. citrullifolium*. One of the anthers is quite large and petaloid. Ovary is bicarpellary, syncarpous, bilocular and superior with swollen axile placenta. Stigma is bilobed in *S. aethiopicum*, *S. citrullifolium*, *S. khasianum* and *S. sisymb-*

rifolium, while 3-lobed in S. integrifolium. Heterostyly is common in S. aethiopicum, S. integrifolium, S. khasianum and S. sisymbrifolium.

4- The anthers are quadrangular in transection. The development of anther wall layers conforms to the Dicotyledonous type in S. aethiopicum, S. citrullifolium, S. integrifolium and S. sisymbrifolium and Basic type in S. khasianum. Anther wall layers comprise the epidermis, endothecium, middle layers and tapetum. The epidermis is single layered. Endothecium is 1-3 layered in S. aethiopicum, 2-3 layered in S. citrullifolium, S. khasianum and S. sisymbrifolium and 3-4 layered in S. integrifolium. Endothecium is devoid of fibrous thickenings except at the tip region. Middle layers are ephemeral and 1-2 layered in S. aethiopicum and S. citrullifolium, 2-layered in S. integrifolium and S. khasianum and 1-3 layered in S. sisymbrifolium.

Tapetum is of dual origin and is generally single layered in all the five species described here. Occasionally at places it becomes two layered in S. sisymbrifolium. Tapetal cells are 1-2 nucleate in S. aethiopicum, S. khasianum and S. sisymbrifolium, 1-4 nucleate in S. citrullifolium and upto 6-nucleate in S. integrifolium. In S. sisymbrifolium the tapetal cells are filled with Ubish granules.

The wall of the dehisced anther comprises an epidermis and few layers of endothecium. Anther dehisces by apical pore in S. integrifolium, S. khasianum and S. sisymb-

rifolium whereas in S. aethiopicum and S. citrullifolium the anthers dehisce by apical pore as well as pores formed at regular intervals on longitudinal suture.

5- The male archesporium is hypodermal in origin and uniseriate. The divisions in all the microspore mother cells of an anther may not be synchronous. Chromosomal abnormalities at meiosis I and II have been observed in S. citrullifolium, S. integrifolium, S. khasianum and S. sisymbrifolium. The microspore tetrads are generally tetrahedral, occasionally decussate. Rarely the tetrads are isobilateral in S. aethiopicum, S. citrullifolium and S. integrifolium and rhomboidal and isobilateral in S. khasianum and S. sisymbrifolium. Rarely one or two microspores in a tetrad may be deformed in S. citrullifolium.

Generally the pollen grains are tricolporate in S. aethiopicum, S. citrullifolium, S. integrifolium, S. khasianum and S. sisymbrifolium. Bicolporate and multicolporate pollen grains have also been observed in S. integrifolium. Variations in the size of nuclei have also been observed in S. citrullifolium, S. integrifolium and S. khasianum.

Pollen grains are shed at 2-nucleate stage in S. citrullifolium, S. khasianum and S. sisymbrifolium while in S. aethiopicum and S. integrifolium, they are shed at 3-nucleate stage. Polysiphonous condition and in situ germination of pollen grains are common in S. citrullifolium.

Pollen viability in S. aethiopicum, S. citrullifolium, S. integrifolium, S. khasianum and S. sisymbrifolium is 24.58%, 66.33%, 87.46%, 92.44% and 39.41% respectively.

The size of the pollen grains measured is 20.45 μ in S. aethiopicum, 21.86 μ in S. citrullifolium, 16.87 μ in S. integrifolium, 22.8 μ in S. khasianum and 19.05 μ in S. sisymbrifolium.

6- The ovules are anatropous, unitegmic and tenuinucellate in S. aethiopicum, S. citrullifolium, S. integrifolium, S. khasianum and S. sisymbrifolium and rarely orthotropous in S. khasianum. The endothelium differentiates at 2-nucleate embryo sac stage in S. citrullifolium, S. integrifolium, S. khasianum and S. sisymbrifolium whereas in S. aethiopicum it differentiates at functional megaspore stage. The endothelium persists upto maturation of seed in S. sisymbrifolium, while in other four species it degenerates during the seed development. Hypostase is common in the species described here. It persists upto mature embryo sac stage and degenerates after fertilization.

7- The single celled female archesporium is hypodermal in origin in S. aethiopicum, S. citrullifolium, S. integrifolium, S. khasianum and S. sisymbrifolium. Occasionally it may be 2-celled in S. citrullifolium, 2-3 celled in S. aethiopicum and S. khasianum and upto 4-celled in S. integrifolium and S. sisymbrifolium. Accessory archesporial cells have also

been observed at various stages of megasporogenesis and megagametogenesis in S. aethiopicum, S. citrullifolium, S. integrifolium, S. khasianum and S. sisymbrifolium. Female archesporial cell directly functions as megaspore mother cell. It undergoes meiosis and produces megaspore tetrad. The megaspore tetrads are generally linear in S. aethiopicum, S. citrullifolium, S. integrifolium, S. khasianum and S. sisymbrifolium. Sometimes the megaspore tetrads may be T-shaped in S. aethiopicum, S. integrifolium and S. sisymbrifolium and rarely inverted T-shaped in S. aethiopicum and S. citrullifolium.

The chalazal megaspore remains healthy and rest three degenerate in all the five species described here. Rarely in S. citrullifolium the micropylar megaspore remains healthy and rest three degenerate. Variations in the number and position of healthy megaspores in a tetrad have been observed in S. aethiopicum, S. citrullifolium, S. integrifolium, S. khasianum and S. sisymbrifolium.

8- Development of female gametophyte conforms to Monosporic, 8-nucleate and Polygonum type in the present investigation. Egg apparatus consists of two synergids and an egg cell. The polar nuclei fuse forming secondary nucleus prior to the entry of the pollen tube into the embryo sac. The antipodal cells are ephemeral and degenerate after fertilization. Variations in the number and organization of embryo sac nuclei have been observed in S. aethiopicum, S. citrulli-

folium, S. integrifolium, S. khasianum and S. sisymbrifolium. Occurrence of twin sacs is a common feature in the species described here.

9- Pollination is anemophillous. Fertilization is porogamous. One synergid is destroyed during the entry of the pollen tube into the embryo sac. The other synergid is also destroyed during the act of fertilization. One male gamete fuses with the egg and the other with the secondary nucleus in S. aethiopicum, S. citrullifolium, S. integrifolium, S. khasianum and S. sisymbrifolium.

10- The development of endosperm is ab initio Cellular. The first division in the primary endosperm cell is transverse forming a primary micropylar and primary chalazal endosperm chambers in S. aethiopicum, S. citrullifolium, S. integrifolium, S. khasianum and S. sisymbrifolium. Occasionally the first division is longitudinal in S. citrullifolium and S. sisymbrifolium. The division in both the primary endosperm chambers is longitudinal forming 4-celled endosperm in S. aethiopicum, S. citrullifolium, S. khasianum and S. sisymbrifolium. In S. integrifolium the primary micropylar endosperm chamber divides longitudinally while primary chalazal chamber transversely forming four cells arranged in a T-shaped manner. The division in both the cells of the micropylar chamber is longitudinal in S. integrifolium, S. khasianum and S. sisymbrifolium and transverse in S. aethiopicum and S. citrullifolium. The division in two juxtaposed cells of the chalazal endosperm

chamber is longitudinal in S. aethiopicum and transverse in S. khasianum and S. sisymbrifolium, whereas in S. citrullifolium a definite sequence is not observed.

The cells of the endosperm in the early stages of development possess vacuolated cytoplasm. At maturity the vacuoles disappear and the cytoplasm becomes rich in reserve food. Cells of mature endosperm develop cellulosic thickenings on their walls in S. aethiopicum and S. khasianum.

11- The zygote divides when sufficient amount of endosperm is formed in S. aethiopicum, S. citrullifolium, S. khasianum and S. sisymbrifolium. While in S. integrifolium the zygote divides when the endosperm is 7-10 celled.

The proembryonic tetrad is linear and the embryogeny conforms to the Myosotis variation of Chenopodiad type in S. aethiopicum and S. integrifolium and Nicotiana variation of Solanad type in S. citrullifolium, S. khasianum and S. sisymbrifolium.

Occasionally the embryogeny conforms to the Myosotis variation of Chenopodiad type in S. citrullifolium and S. sisymbrifolium and Nicotiana variation of Solanad type in S. integrifolium. Rarely the proembryonic tetrad is T-shaped in S. aethiopicum and S. integrifolium and the embryogeny conforms to the Onagrad type.

Variations in the size and number of cotyledons have also been observed in S. integrifolium. Adventive embryony has been observed in S. citrullifolium. In addition to the

zygotic embryos a number of adventive embryos may develop from the cells of endothelium and fill up the embryo sac cavity. In such cases most of the endosperm is consumed which results in the degeneration of zygotic as well as endothelial embryos. The degeneration of zygotic or endothelial embryos may be due to lack of proper nutrition as endosperm does not develop further and is consumed by the endothelial embryos. Thus the resulting seeds are abortive. Cleavage polyembryony has been observed in S. integrifolium.

12- The ontogeny and structure of seed have been described. Anatomically the seed comprises a seed coat, persistent endosperm and mature curved dicotyledonous embryo. The epidermis is the main protective layer and constitute the seed coat in S. aethiopicum, S. citrullifolium, S. integrifolium and S. khasianum, while in S. sisymbrifolium the seed coat comprises an epidermis and persistent lignified single layered endothelium. The cells of the epidermis develop sclerotic thickenings in the inner portion while the outer regions develop rod-like thickenings.

The cells of persistent endosperm possess starch grains and reserve food material. In S. citrullifolium, S. khasianum and S. sisymbrifolium the endosperm extends between the coiled embryo and this part of endosperm is characterized by a comma head and a slender comma stem.

The affinities of the Solanaceae with the allied families on the basis of embryological features have been

discussed. The evolutionary trends in the genus Solanum itself have been brought out.

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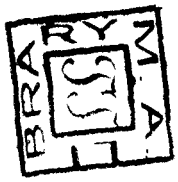

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FAIQ A. KHAN
M. Sc., M. Phil.

BOTANY DEPARTMENT
Aligarh Muslim University
ALIGARH-202001 (INDIA)

Dated...July..30,...1983.

THESIS SECTION

"He it is WHO sendth down water from the sky, and therewith we bring forth vegetation of every kind; We bring forth the green buds from which are derived thick-clustered grains, ... observe upon the fruit thereof when they (plants) bear fruits, and upon its ripening. Lo! here in verily are portents for people who believe".

AL-QUR'AN

(Al-An'am: 12: 100)

DR. SAEED A. SIDDIQUI
READER

BOTANY DEPARTMENT
Aligarh Muslim University
ALIGARH-202001 (INDIA)

Dated 30.7.1983

CERTIFICATE

This is to certify that the work presented in this thesis entitled "The embryology of some Solanaceae" is the original piece of research work carried out by Mr Faiq A. Khan under my supervision and guidance and has not been submitted elsewhere for the award of any other degree or diploma.

(Saeed A. Siddiqui)

FAIQ A. KHAN
M. Sc., M. Phil.

BOTANY DEPARTMENT
Aligarh Muslim University
ALIGARH-202001 (INDIA)

Dated...July 30,...1983.

ACKNOWLEDGEMENT

I take this opportunity to express my deepest sense of gratitude to my supervisor Dr. Saeed A. Siddiqui, Reader, Department of Botany, Aligarh Muslim University, Aligarh for his unceasing encouragement and valuable guidance during the course of the preparation of this thesis.

I am grateful to Prof. S.K. Saxena, Chairman, Deptt. of Botany, Aligarh Muslim University, Aligarh for providing library and research facilities.

I remain indebted to my laboratory colleagues Dr. Naiseuddin Ahmad, Dr. Shama P. Siddiqui, Mrs. Naeema Khanum, Miss. Anjum Afshan, Messrs. Saeed Ahmad, M.Y.K. Ansari, Saiful Islam Qurishi for their generous help and encouragement.

Thanks are also due to U.G.C. for the award of Junior and Senior Research Fellowships.

Finally I wish to thanks my friends Messrs. Bilal A. Zaidi, Sarfaraz Hadi, Anwar Zaheer, Maharaj Nawaz Khan, Seraj A. Khan, Mohd. Suhail and Imran Masood for their co-operation and encouragement.

(Faiq Ahmad Khan)

PREFACE

The main thesis deals with the embryology of *Solanum aethiopicum* L., *S. citrullifolium* A.Br., *S. integrifolium* L., *S. khasianum* Clarke and *S. xiavmbrifolium* Lam.

Following research papers have also been published.

(I) Effect of gamma-irradiation on the epidermis of *Capsicum annuum* L.
Plant Sci. 11:31-34, 1979 (With Raisuddin Ahmad and Saeed A. Siddiqui).

(II) Effect of gamma rays on germination seedling growth and epidermal tissues of *Phaseolus mungo* L.
Sci. & Environ. 1:85-90, 1979 (With Saeed A. Siddiqui, Raisuddin Ahmad and Saeed Ahmad).

(III) Effect of gamma-irradiation on seed germination, seedling growth and cotyledonary stomata of *Abelmoschus esculentus* Moench.
Proc. Symp. Environ. Biol. 249-252, 1979.

(IV) Studies on the effect of gamma-irradiation on *Luffa acutangula* Roxb.
Sci. & Environ. 2:71-73, 1980 (With Saeed A. Siddiqui, Raisuddin Ahmad and Saeed Ahmad).

(V) The structure and development of male and female gametophytes in *Solanum khasianum* Clarke.
Sci. & Environ. 3(1):21-25, 1981 (With Saeed A. Siddiqui).

(VI) Development of endosperm, embryo and seed in *Solanum khasianum* Clarke.
Geophytology 11:154-157, 1981 (With Saeed A. Siddiqui and Shama P. Siddiqui).

(VII) The development of gametophytes in *Hamelia sphaerocarpa* Jacq.
Jour. Sci. Res. 4:47-49, 1982 (With Shama P. Siddiqui and Saeed A. Siddiqui).

(VIII) Effect of gamma-irradiation on germination, seedling growth and cotyledonary stomata of *Cucumis sativus* Linn.
Allahabad farmer (accepted), 1982 (With Saeed A. Siddiqui, Raisuddin Ahmad and Saeed Ahmad).

(IX) Chromosomal abnormalities in natural population of *Solanum khasianum* Clarke.
Plant Sci. (accepted), 1982 (With Saeed A. Siddiqui & M.Y.K. Ansari).

(X) Effect of gamma-irradiation in *Solanum melongena* L. CV. Pusa Kranti.
Indian J. Forestry (accepted 1983)
(With Saeed A. Siddiqui & Raisuddin Ahmad).

CONTENTS

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INTRODUCTION

The development of thought on the classification of the Solanaceae is traced from the classical times to the present day, with particular reference to the boundaries of the family, its relationship to others such as Nolanaceae and Scrophulariaceae, and the general arrangement of tribes and genera. However, divergent views have been put forward regarding the exact taxonomic relationships of the family Solanaceae. Bartling (1830) placed Solanaceae in an alliance of families having sympetalous corollas, epipetalous stamens, and connate carpels . It is placed in the order polemoniales by Bentham and Hooker (1873-1876), Bessey (1893), Gunderson (1950), Benson (1957) and Cronquist (1968). In Bentham and Hooker's classification Convolvulaceae precedes Solanaceae. In Bessey's system it is placed between polemoniaceae and Nolanaceae. Gunderson (1950) is of the openion that Solanaceae is better placed between Nolanaceae and Scrophulariaceae. The Polemoniales of Benson (1957) includes Convolvulaceae, Polemoniaceae, Hydrophyllaceae, Boraginaceae, Lennoaceae, Nolanaceae and Solanaceae. According to Takhtajan (1966) Solanaceae have closest relationship with Scrophulariaceae. On the other hand the Polemoniales of Cronquist (1968) includes Nolanaceae, Solanaceae, Convolvulaceae, Cuscutaceae, Menyanthaceae, Polemoniaceae, Hydrophyllaceae and Lennoaceae.

Engler and Prantle (1898), Wettstein (1935), Rendle (1952) and Melchior (1964) proposed the order Tubiflorae which includes Solanaceae alongwith Nolanaceae, Convolvulaceae and Scrophulariaceae. Porter (1959) does not agree with the position and placed it in the order Scrophulariales together with Bignoniaceae, Orobanchaceae, Lentibulariaceae and Scrophulariaceae. On the other hand Hutchinson (1959, 1964) put forward another order Solanales which forms the natural assemblage of Solanaceae, Convolvulaceae and Nolanaceae. Later, Hutchinson (1969) proposed a family Salpiglossidaceae as an intermediate between Solanaceae and Scrophulariaceae. Wettstein (1892) and Corner (1976) have indicated belief that the Tubiflorae is an unnatural assemblage of families, but the recent divisions into smaller orders may not have meant improvement.

The family Solanaceae is one of the largest Bicarpellatae families having 90 genera and about 2,000 species (Willis, 1966). According to D'Arcy (1976) "The Solanaceae embraces some 84 genera and almost 3,000 species which occur on every vegetated continent in the world. Wettstein (1935) sub divided Solanaceae into five tribes; Nicandreae, Solaneae, Datureae, Cestreae and Salpiglossideae.

The genus Solanum belongs to the tribe Solaneae of Solanaceae. It is one of the largest genera in plant kingdom being represented by approximately 2,000 species (Ghile, 1976). The genus Solanum shows great heterogenity in habit, morphology,

embryology, fruit and seed structure. It has attracted the attention of botanist for a long time due to its ornamental, food and medicinal values.

Inspite of the morphological and embryological peculiarities about half a scrore of its species have been worked out embryologically by Nanetti (1912), Young (1922, 1923), Bhaduri (1932, 1936), Dnyansagar and Cooper (1960), Saxena and Singh (1969a,b), Mohan (1970) and Ahmad and Siddiqui (1981). A perusal of earlier literature on the embryology of Solanums shows the paucity of adequate data on the comparative morphology and embryology as well as sequential development of seed in majority of the described species.

Thus considering the embryological peculiarities of the investigated Solanums and the number of species worked out it was considered worthwhile to investigate some more species of the genus Solanum and see if the embryological features could be helpful in tracing the evolutionary trends within the genus itself and the relationship with the allied families.

MATERIALS AND METHODS

The identified seeds of *Solanum aethiopicum* L. and *S. citrullifolium* A.Br. were acquired by Dr. Saeed A. Siddiqui from Prof. J.G. Hawkes, Department of Botany, University of Birmingham U.K. The seeds were sown in pots and plants were raised.

Flower buds and fruits of different developmental stages of *S. aethiopicum* L., *S. citrullifolium* A.Br., *S. integrifolium* L., *S. khasianum* Clarke and *S. sisymbrifolium* Lam. were collected and fixed in formalin-acetic-alcohol. The mature dry seeds of all the five species were water boiled for few hours and then transferred to saturated picric acid solution at room temperature for 2-4 weeks depending upon the hardness of the seed. Later, they were washed in running water till the traces of the picric acid were completely removed. The treated seeds were stored in 70% alcohol.

The materials were dehydrated in alcohol-xylol series or TBA series and embedded in paraffin wax. The sections were cut at 8-12 μ and mounted on the slides. The preparations were stained in safranin and fast green combination and mounted in Canada balsam.

For microsporogenesis and pollen viability the flower buds were fixed in Carnoy's fluid for 40 minutes, then transferred to propionic acid saturated with ferric acetate.

After 24 hours the buds were transferred to 70% alcohol. Anther squashes were made for microsporogenesis and pollen viability using 0.5% propionocarmine. The slides of microsporogenesis were made permanent in NBA series and finally mounted in Canada balsam.

REVIEW OF PREVIOUS WORK

A considerable amount of literature has accumulated on the embryology of Solanaceae during the last three decades. The available literature on the embryology of Solanaceae was first reviewed by Schurhoff (1926). A number of excellent reviews have also been published (Schnarf, 1931; Bhaduri, 1935, 1936; Davis, 1966; and Vargheese, 1967). Johansen (1950) has summarized the literature on the embryogeny of the family. Besides, the monographs on *Nicotiana* (Goodspeed, 1954) and *Datura* (Avery *et al.*, 1959) contain good deal of information on the embryology of these two genera. The detailed review on the embryology of Solanaceae is described in the following pages.

Organogeny

The differentiation of floral parts takes place in acropetal succession in *Capsicum* (Augustin, 1907), *Solanum tuberosum* (Young, 1922), *Solanum* and *Lycopersicum* (Smith, 1935), *Capsicum frutescens* (Cochran, 1938) and *Capsicum annuum* Var. minimum and *Capsicum annuum* Var. annuum (Munting, 1974).

Microsporangium, Microsporogenesis and Male gametophyte

The microsporangium is tetrasporangiate in Solanaceae. The development of anther wall layers in the investigated Solanaceae conforms to the Dicotyledonous type of Davis (1966) except in Withania somnifera (Mohan Ram and Kamini, 1964), where it follows Basic type of Davis (1966). However, Dicotyledonous and Basic types of anther wall development have also been reported in the members of Solanaceae by Singh and Saxena (1968). Monocotyledonous type of anther wall development has also been described in Nicotiana (Jos and Singh, 1968). The epidermal cells of a mature anther are tangentially elongated. The protoplast of the epidermal cells shrinks at the shedding time of the pollen grains and their outer tangential walls develop cuticular dentation in Lycium europaeum (Jain, 1956). Ample amount of starch is deposited in the cells of epidermis in Withania somnifera (Mohan Ram and Kamini, 1964). The epidermis persists in mature anther and at maturity its outer wall becomes cutinized.

The hypodermal endothecium is generally single layered in all the investigated species of Solanaceae except Nicotiana tabacum and N. glutinosa (Jos and Singh, 1968) and Solanum trioncetrum (Ahmad and Siddiqui, 1981) where it varies from 1-3 layered. The cells of the endothecium increase in size and their cytoplasm becomes vacuolated at maturity. The fibrous thickenings generally develop in the endothecium

except in genera where dehiscence is porous (Davis, 1966). The endothecium persists and fibrous thickenings develop only in the apical region in Solanum nigrum (Saxena and Singh, 1969a). However, the cells of endothecium were found devoid of fibrillar thickenings in Solanum tuberosum (Young, 1923), S. macranthum (Mohan, 1970) and S. trigonatrum (Ahmad and Siddiqui, 1981). The middle layers are ephemeral (See Davis, 1966).

The tapetum is glandular in Solanum tuberosum (Young, 1923), Lycium europaeum (Jain, 1956), Capsicum frutescens (Lengel, 1960), Withania somnifera (Mohan Ram and Kamini, 1964), Nicotiana tabacum, N. rustica, N. alata, N. glutinosa, N. glauca, N. megalosiphon, N. trigonophylla, N. longiflora and N. plumbaginifolia (Joe and Singh, 1968), Solanum nigrum, S. americanum, S. nodiflorum, S. luteum, S. sarrachoides and S. villosum (Saxena and Singh, 1969b). According to Prasad and Singh (1978), the tapetum degenerates during gametogenesis in Nicandra physaloides and its nuclei fuse to form large polyploid masses before finally collapsing. Endomitosis has been described in the tapetal cells of Lycopersicon esculentum (Brown, 1949), Solanum nigrum and S. dulcamara (Turala and Werytkiewicz, 1964). However, Rybchenko (1963) did not observe endomitosis. Varghese (1967) reported amoeboid tapetum in Datura stramonium. The cells derived from the anther tissue towards the connective side are conspicuous and assume the characteristics of tapetum, thus the tapetum

encloses the sporogenous tissue. Its cells are generally radially elongated.

The hypodermal male archesporium is generally single layered but a 2-layered horse-shoe-shaped archesporium has been reported in Potato (Young, 1923). The microspore mother cells undergo usual meiotic divisions. The microspore tetrads are generally tetrahedral in Solanum tuberosum (Khan, 1951), Withania somnifera (Mohan Ram and Kamini, 1964), Nicotiana (Jos and Singh, 1968), Solanum nigrum, S. americanum, S. nodiflorum, S. luteum, S. sarachoides and S. villosum (Saxena and Singh, 1969b) and S. triquetrum (Ahmad and Siddiqui, 1981). Sometimes the microspores in a tetrad may be arranged in a linear fashion in Solanum tuberosum (Khan, 1951). The pollen grains are usually uninucleate rarely binucleate at the time of anthesis (Barnard, 1949), while in Lycium europaeum (Jain, 1956), Withania somnifera (Mohan Ram and Kamini, 1964), Nicotiana (Jos and Singh, 1968), Solanum nigrum, S. americanum, S. nodiflorum, S. luteum, S. sarachoides and S. villosum (Saxena and Singh, 1969b) and Solanum triquetrum (Ahmad and Siddiqui, 1981) the pollen grains are shed usually at 2-celled stage. However, the pollen grains may occasionally be 3-celled at shedding stage in Nicotiana (Pedubnaja-Arnoldi, 1936) and Capsicum frutescens (Lengel, 1960).

The earlier literature on the palynology of Solanaceae was reviewed by Erdtman (1952). Nair (1965) has examined the pollen morphology in Atropa belladonna, Datura metel, D.

stramonium, D. suaveolens, Hyoscyamus niger, Nicandra physaloides, Solanum pseudocapsicum and S. verbascifolium. The pollen morphology of 93 species belonging to 28 genera of the family has been described by Basak (1967).

Ghile and Sowunmi (1976) studied in detail the pollen morphology of Nigerian Solanums. According to them the pollen grains of 19 taxa of Nigerian Solanum were found to have very similar apertural status i.e. 3-colporate. A great deal of resemblance in the characteristics of colpi and ora was also observed. There are major differences in overall size and shape. The morphological features of the pollen grains are so distinct to permit the identification of the various species, subspecies and varieties.

The pollen grains in the investigated Solanaceae are 3-5 (-6) colpate, colporidate and rarely non aperturate (See Varghese, 1967). The tricolpate and spheroidal pollen grains with smooth exine are reported in Lycium europaeum (Jain, 1956), Withania somnifera (Mohan Ram and Kamini, 1964), Solanum nigrum, S. americanum, S. luteum, S. nodiflorum, S. xanthocarpum and S. villosum (Sarma and Singh, 1969b). The mature pollen grains are globular in shape with smooth exine and intine and have four germ pores in Nicotiana (Joe and Singh, 1968).

Variations in the diameter of pollen grains of different species of Nicotiana have been observed by Joe and Singh (1968). The diameter of the pollen grains was 29 μ in Nicotiana

tabacum, N. glutinosa, N. longiflora and N. plumbaginifolia and about 36 μ in N. rustica, N. glauca and N. alata, while about 42 μ in N. megalosiphon.

Polysiphonous germination and branched pollen tubes were reported by Krishnamurty and Appa Rao (1958) in the hybrid of Nicotiana longifolia X N. alata. Vasil (1964) described pollen germination of Capsicum annuum, Solanum melongena and S. tuberosum. Lunyeva, pedubnaja-Arnaldi and Bhandari (1970) made cytological and histochemical investigations on Nicotiana alata, N. glauca and their hybrid. They recorded considerable meiotic abnormalities and high percentage of pollen sterility in F_1 hybrids.

The formation of resorption tissue at the site of dehiscence in 10 species of Solanaceae was described for the first time by Namikawa (1919). Singh and Saxena (1968) have described the method of dehiscence in 20 species belonging to 7 genera of the family. They reported the presence of resorption tissue in Lycopersicum, Lycium, Capsicum, Physalis and Solanum but a distinct resorption tissue is not observed in Datura. The anther dehisces longitudinally in Solanum nigrum, S. xanthocarpum, S. surattense, S. luteum, S. xanthocidum and S. villosum and well organised resorption tissue, resorption cavity, resorption passage and stomium develop at the site of dehiscence (Saxena and Singh, 1969b). However, the dehiscence of anther is passive in Solanum tuberosum (Young, 1923), S. trilobatum (Hussain, 1968) and S. xanthocarpum (Mohan, 1970).

Megasporangium, Megasporogenesis and Female Gametophyte

The ovules are anatropous in Nicotiana rustica, N. tabacum and Datura stramonium (Chatin, 1874), Lycopersicum esculentum (Cooper, 1931), Solanum tuberosum (Rees-Leonard, 1935), Nicotiana plumbaginifolia and Petunia nyctaginiflora (Bhaduri, 1935), Pepper (Cochran, 1938), Solanum section tuberarium (Walker, 1955), Lycium europaeum (Jain, 1956), Solanum dhurmia (Dnyansagar and Cooper, 1960), Exacallia dominga (Mohan, 1966) and in Nicotiana glutinosa, N. glauca, N. longiflora, N. megalosiphon, N. trigonophylla and N. alata (Joe and Singh, 1968). The ovule in S. tuberosum (Young, 1923) in not, however, of typical anatropous type, since the embryo sac is considerably curved, suggesting a transition to the campylotropous form. Rees-Leonard (1935) described amphitropous ovules in S. tuberosum.

Hemianatropous ovules have been described in Browallia americana, Datura fastuosa, Lycopersicum esculentum, Physalis minima, P. [illegible]-Salpiglossis sinuata, Solanum nigrum and Withania somnifera (Bhaduri, 1935) and Solanum trigonatrum (Ahmad and Siddiqui, 1981).

In Capsicum (Bhaduri, 1935) the ovules are perfectly campylotropous. The ovules are generally anacampylotropous in S. nigrum, S. americanum, S. luteum, S. nodiflorum, S. xanthocarpum and S. villosum (Saxena and Singh, 1969b) and S. nigrum (Mohan, 1970).

The single celled female archesporium is hypodermal in origin (Schnarf, 1931; Davis, 1966). It directly functions as megaspore mother cell. The rare occurrence of 2-celled archesporium is reported in Solanum nigrum, S. americanum, S. luteum, S. nodiflorum and S. saracheides (Saxena and Singh, 1969b) and S. nigrum (Mohan, 1970), whereas 2-celled female archesporium is of common occurrence in S. villosum (Saxena and Singh, 1969b). Multicellular archesporium is a characteristic feature of Datura (Glisic, 1928; Avery et al., 1959) and Solanum tuberosum (Rees-Leonard, 1935). Multicellular archesporium also may occur in Solanum melongena (Bhaduri, 1932), Lycopersicum esculentum, Physalis peruviana, Nicotiana plumbaginifolia, Salpiglossis sinuata and Brunfelsia americana (Bhaduri, 1935) and Solanum triquetrum (Ahmad and Siddiqui, 1981).

The megaspore tetrads are generally linear in Solanum melongena (Bhaduri, 1932), Lycopersicum esculentum (Cooper, 1931), Solanum nigrum, Physalis minima, P. peruviana, Withania somnifera, Datura fastuosa, Petunia nyctaginiflora (Bhaduri, 1935), Lycium europaeum (Jain, 1956), Browallia demissa (Mohan, 1966), Nicotiana (Jos and Singh, 1968), Solanum nigrum (Mohan, 1970), Nicandra physaloides (Prasad and Singh, 1978), Solanum triquetrum (Ahmad and Siddiqui, 1981).

The chalazal megaspore is functional in all the investigated species of Solanaceae. However, micropylar megaspore is functional instead of chalzal one in Solanum nigrum and S. turbinatum (Krüger, 1932). The two chalazal megaspores remain healthy

in Lycopersicum esculentum (Cooper, 1931), Solanum melongena (Bhaduri, 1932) and Physalis (Bhaduri, 1935). According to these authors, this is probably an additional cause for the development of twin embryo sacs. Hofmeister (1858) was first who observed mature embryo sac in Hyoscyamus orientalis, Scopolina atropoides and Salpiglossis picta. Jönsson (1881) described the development of embryo sac in Saracha jaltomata. Polygonum type of embryo sac development has been recorded in Cestrum splendens and Nicotiana tabacum (Guignard, 1882), Atropa belladona (Souèges, 1907), Nicotiana (Palm, 1922), Delitabac and Hyoscyamus niger (Svensson, 1926), Lycopersicum esculentum (Cooper, 1931), Capsicum annuum (Banerji, 1931), Solanum melongena (Bhaduri, 1932), Nicotiana rustica (Peraidsky and Modilewski, 1935), Duboisia hiechhardtii, D. myeporoides (Barnard, 1949), Lycium europaeum (Jain, 1956), Nicotiana tabacum, N. rustica, N. glutinosa, N. glauca, N. macrosiphon, N. trigonophylla, N. plumbaginifolia, N. longiflora and N. alata (Joe and Singh, 1968), Solanum nigrum (Saxena and Singh, 1969a), S. macranthum (Mohan, 1970), Withania somnifera (Bhaduri, 1935; Mohan Ram and Kamini, 1964; Ariz et al., 1972) and S. trigustrum (Ahmad and Siddiqui, 1981). Lengel (1960) described bisporic embryo sac in Capsicum frutescens var. Japanese variegated ornamental, whereas Mutafjan (1964) described monosporic type of embryo sac development in Capsicum. The Allium type of embryo sac occurs in Capsicum frutescens, Cestrum elegans, Nicotiana ditacia and N. rustica (See Davis, 1966). Nanetti (1912) and

Young (1923) found Lilium type of embryo sac and as pointed out by Mohan Ram and Kamini (1964) this variation refers to the modern Adoxa type. Modilewski (1935) reported Scilla type of embryo sac development in Nicotiana glauca.

Occasional occurrence of twin embryo sacs has been observed in Solanum tuberosum (Young, 1922), S. melongena (Bhaduri, 1932), Withania somnifera, Physalis minima (Banerji and Bhaduri, 1933), S. nigrum, S. americanum, S. luteum, S. nodiflorum, S. sarachoides and S. villosum (Saxena and Singh, 1969b).

The synergids have long acute beaks fitting into the micropylar end of the embryo sac in the investigated species of the family. The synergids exhibit filiform apparatus in Lycopersicum esculentum (Cooper, 1931) and Solanum tuberosum (Rees-Leonard, 1935). However, Young (1923) and Svensson (1926) have not described the occurrence of filiform apparatus in Solanum tuberosum and Hyoscyamus niger respectively. The synergids are elongated, pyriform and hooked in Solanum phureja (See Davis, 1966).

The three antipodals which occupy the chalazal end of the embryo sac are usually ephemeral. They enlarge and persist during endosperm formation in Atropa belladona, Datura metal and Solanum phureja (See Davis, 1966). A case of inversion of the embryo sac with a characteristic egg apparatus at the chalazal end has been noted in Nicotiana (Goodspeed, 1947) and Lycium

europaeum (Jain, 1956). This embryo sac has three antipodal like cells at the micropylar end. In Lycopersicum and Datura(Bhaduri, 1935) the two lower antipodals are long and rectangular and fit in the chalazal end of the embryo sac, while the third antipodal is comparatively broader and lie above the two. However, the two antipodals have been found to lie above a broad basal antipodal cell in Cestrum (Bhaduri, 1935). The arrangement of the antipodals seems to depend on the plane of orientation of the spindles at the chalazal end of the embryo sac. The antipodals are big and uni-nucleate in Solanum dulcamara, Atropa belladona and Nicotiana tabacum (Schnarf, 1931). The antipodals are small and degenerate early in Hyoscyamus niger (Svensson, 1926) and Datura laevis (Bhaduri, 1935) and persist long after fertilization in Datura metel (Bhaduri, 1935). The antipodals could be seen after fertilization in Lycopersicum and Nicotiana (Bhaduri, 1935). Souèges (1907) stated that the chalazal groove of the embryo sac is a haustorium and the antipodal cells act as secretory organs, which actively secrete chemical substances and help in digesting the nucellar tissue.

Accumulation of starch grains within the embryo sac has been observed in Cestrum (Bhaduri, 1935), Nicotiana (Dahlgren, 1939), Petunia (Cooper, 1946) and Solanum demissum (Walker, 1955). Svensson (1926) has observed starch kernels in the integumentary tapetal cells in Hyoscyamus niger, whereas in S. tuberosum (Williams, 1955) and Solanum phureja (Dnyansagar and Cooper, 1960) starch grains are not present in the embryo sac at the time of fertilization.

Fertilization

The fertilization is porogamous in Solanaceae. Normally the pollen tube passes through the micropyle and enters the megagametopyte between the synergid and egg. In some exceptional cases the tip of the pollen tube had divided into two short branches in Petunia (Cooper, 1946) and Nicotiana hybrid (Varghese, 1967). One branch becoming closely appressed to the egg and the other extending in the direction of the polar nuclei, so that the two male gametes reach their destinations by way of these separate branches. Double fertilization has been observed in Petunia (Cooper, 1946), Solanum tuberosum Var. chippewa (Williams, 1955), S. nigrum (Saxena and Singh, 1969a) and Nicandra physaloides (Prasad and Singh, 1978). The pollen tube enters the sac 72 to 96 hours after pollination in Petunia (Ferguson, 1927). But according to Cooper (1946) fertilization occurs 24 hours after pollination in ovules situated at the top of the ovary while the basal ones are fertilized 32 hours after pollination in Petunia. The process of syngamy and triple fusion takes about 24 hours to 48 hours after pollination in Solanum species (Walker, 1955). However, triple fusion occurs between 24 and 72 hours after pollination in Solanum phureja (Dnyansagar and Cooper, 1960). Occasionally the fusion of male gamete with the egg nucleus does not occur, although the endosperm may become several celled in S. phureja (Dnyansagar and Cooper, 1960).

Endosperm

Hofmeister (1858) for the first time observed nuclear type of endosperm in Hyoscyamus orientalis, Salpiglossis and Scopolia atropoides. Nuclear type of endosperm has also been reported in Schizanthus pinnatus (Samuelsson, 1913 Dahlgren, 1923), Capsicum (Crété, 1961c; Mutafjan, 1964) and Solanum trigustrum (Ahmad and Siddiqui, 1981).

The development of Cellular endosperm is most common in Solanaceae and reported in Atropa, Datura, Physochlaena, Salpiglossis variabilis and Scopolia (Dahlgren , 1923), Lycopersicum esculentum (Bhaduri, 1936), Petunia (Cooper, 1946), Solanum species (Wangenheim, 1957), S. phureja (Dnyansagar and Cooper, 1960), Hibbonia somnifera (Mohan Ram and Kamini, 1964), Nicotiana (Jos and Singh, 1968), S. nigrum, S. americanum, S. luteum, S. pauciflorum, S. saracheides and S. villosum (Saxena and Singh, 1969b), S. macranthum (Mohan, 1970) and Nicandra physaloides (Prasad and Singh, 1978). Svensson (1926) reported ab initio Cellular endosperm in 22 members in Solanaceae. In Hyoscyamus niger he observed Cellular as well as Helobial types. Helobial endosperm has also been reported in Duboisia (See Davis, 1966).

In Petunia Ferguson (1927) reported that secondary nucleus divides to form a diploid 2-celled endosperm. Bhaduri (1933) observed this phenomenon in Lycopersicum esculentum and Petunia axillaniflora.

The first division in the primary endosperm nucleus is transverse in Datura laevis (Guignard, 1902), Petunia nyctaginiflora (Cooper, 1946), Withania somnifera (Mohan Ram and Kamini, 1964), Nicotiana tabacum (Jee and Singh, 1968), Solanum nigrum (Mohan, 1970) and Nicandra physaloides (Prasad and Singh, 1978). The second division in both the primary endosperm chambers is transverse producing four cells arranged linearly. On the other hand both the primary endosperm chambers divide by vertical walls in Solanum nigrum (Saxena and Singh, 1969a). In Solanum phureja (Dnyansagar and Cooper, 1960) the first two divisions are vertical resulting in the formation of four large cylindrical cells which are of similar dimensions.

The chalazal haustorium has been observed in Solanum melongena (Magtang, 1936) and S. phureja (Dnyansagar and Cooper, 1960). In S. nigrum (Mohan, 1970) recorded that the cells of two extreme ends ultimately form the chalazal and micropylar haustoria, while the remaining cells give rise to the main body of endosperm.

Embryogeny

The embryogeny in the investigated Solanaceae viz., Solanum tuberosum, Datura stramonium, Physalis minima and Atropa belladonna (Tognini, 1900), Nicotiana, Datura and Atropa (Souèges, 1920a,b; 1922), Nicotiana rustica (Poroidsky and Medilewski,1935; Medilewski, 1937), Physalis minima, Withania somnifera and Petunia

nyctaginiflora (Bhaduri, 1936), Schizanthus and Petunia(Seueges, 1936), Physalis peruviana (Créte, 1954), Solanum demissum(Walker, 1955), Saracha jaltomata (Créte, 1960), Solanum phureja (Dnyansagar and Cooper, 1960), Datura fatula (Créte, 1961a) Browallia demissa (Créte, 1961b), Salpiglossis sinuata (Créte, 1961d), S. nigrum, S. americanum, S. luteum, S. nodiflorum, S. sarachoides and S. villosum (Saxena and Singh, 1969b) and S. triquetrum (Ahmad and Siddiqui, 1981) conforms to the Nicotiana variation of Solanad type. However, embryogeny follows Ongrad type in Capsicum annuum (Créte, 1961c).

The formation of adventive embryos is reported in Nicotiana rustica Var. Brasilia when pollinated with Petunia pollen (Biraghi, 1929). The development of adventitious embryos has been reported by Haberlandt (1931) in Scopolia. Polyembryony has also been observed in Nicotiana plumbaginifolia, Withania somnifera and Petunia nyctaginiflora (Banerji and Bhaduri,1933). The two well developed embryos have been observed in two separate embryo sacs in the same ovule in Nicotiana plumbaginifolia (Banerji and Bhaduri, 1933). Earlier stages in the development of adventitious embryos by the budding of the nucellar cells covering the embryos sac have been observed in Petunia nyctaginiflora and Withania somnifera (Banerji and Bhaduri, 1933). The haploid seedlings were observed during the course of investigation on interspecific hybridization of Nicotiana by Cooper (1943). This made him to suggest that one embryo developed from the synergid and was haploid in origin. Cameron (1949) has

reported a case of polyembryony in Nicotiana tabacum giving rise to two seedlings with different chromosome numbers.

Cleavage of young proembryo has been observed in Nicotiana rustica (Cooper, 1943).

Seed

The most outstanding and exhaustive study of the seed coat anatomy of 46 species belonging to 26 genera of the Solanaceae has been made by Souèges (1907). According to him the fully matured integument is differentiated into the following 3 zones, of which the middle one is divided into two;

(i) Assise externe : the outer epidermis

(ii) Assise interne : the inner epidermis

(iii) Partie moyene : the intermediate layer of cells which consists of two zones.

(i) Zone externe

(ii) Zone interne.

The layers comprising partie moyene lose their contents and mostly disintegrate. Only a few outer most layers persist in seed in greatly compressed form. On the basis of this histological differentiation of these three layers, Souèges (1907) has been able to classify the principal genera under Solanaceae.

Metcalfe (1926) described the structure and development of seed in Solanaceae. A detailed study was made on the ontogeny and structure of seed in Lycopersicum esculentum (Smith, 1935), Capsicum frutescens Var. grossus (Cochran, 1938). Similar studies have been made by Barnard (1949), Dnyansagar and Cooper (1960), Jain (1962) and Czaja (1963, 1965).

The seed coat consists of 4 or 5 layers including the persistent endothelium in Solanum nigrum (Saxena and Singh, 1969a), Solanum macranthum (Mohan, 1970) and Nicandra physaloides (Prasad and Singh, 1978), while seed coat consists of an epidermis and persistent endothelium in Solanum nigrum, S. americanum, S. luteum, S. nodiflorum, S. sarachoides and S. villosum (Saxena and Singh, 1969b). The size and shape of the endothelial cells and the nature of thickenings on their walls vary in different species of Solanums.

The seed coat may or may not be multiplicative, generally reduced to the epidermis and the endothelium. The epidermis is compact layer of cells with more or less undulate or Stellate facets, either with more or less strongly thickened inner and radial walls in Atropa, Brugmallia, Capsicum, Lycium, Mandragora, Nicandra, Nicotiana, Petunia, Solanum and Withania (See Corner, 1976).

The seeds are small, often flattened and discoid, or subquadrate, mostly albuminous, exarillate, in some cases embedded in placental pulp as in Lycopersicum (Smith, 1935),

Solanum nigrum, S. americanum, S. luteum, S. nodiflorum, S. saxatheidea and S. villosum (Saxena and Singh, 1969b) and Solanum nanxanthum (Mohan, 1970). However, the seeds are non glossy, reddish brown to dark brown in colour, with a finely pitted reticulate surface, oval, semiorbicular in outline and flattened laterally in Solanum nemorum (Miller, 1969).

EXTERNAL MORPHOLOGY

SOLANUM AETHIOPICUM L.

S. aethiopicum is an annual herb, erect branched, 60-90 cm high with branched tape root. Stem is branched, herbaceous, cylindrical, solid, with stellate hairs. Leaves alternate, petiolate (petiole 1.4-2.1 cm long), exstipulate, ovate, margin undulate, acute apex, both the surfaces with stellate hairs.

The inflorescence is extra axillary cyme. Flowers pedicellate, ebracteate, complete, bisexual, actinomorphic, hypogynous, white in colour. Sepals five, occasionally 6 or 7, gamosepalous, green inferior, valvate aestivation, campanulate, persistent provided with stellate hairs. Petals five, occasionally 6 or 7, gamopetalous, imbricate aestivation, abaxial surface with stellate hairs, campanulate, white in colour.

Stamens five, occasionally upto 7, polyandrous, connivent , epipetalous, filament short (2.0 mm), flattened, anther yellow 4.0 mm long, basifixed. Dehiscence is porous as well as by pores formed at regular intervals in longitudinal suture.

Ovary bicarpellary, syncarpous, bilocular, numerous ovules with swollen and oblique axile placentation. Heterostyly

has been observed, stigma bilobed, gynoecium measures 1.0 cm. Fruit is a berry, globose, tomato-like, changing green to red on ripening.

Solanum aethiopicum

SOLANUM CITRULLIFOLIUM A.Br.

S. citrullifolium is an annual herb, erect, 60-80 cm high. Tape root profusely branched, stem erect, branched woody, cylindrical, hairy as well as spiny. Leaves alternate, petiolate (2.5-5.0 cm), covered with glandular hairs and spines, exstipulate, subpinnatifid, ovate, apex obtuse, hairy, spines on the vein.

Inflorescence extra axillary cyme. Flowers pedicellate, pedicel spiny, ebracteate, complete, bisexual, zygomorphic, hypogynous and violet in colour.

Sepals five, gamosepalous, covered with glandular hairs and spines, valvate aestivation, inferior, 6 mm long, persistent and accrescent.

Petals five, gamopetalous, zygomorphic, two petal differ in size from remaining three, violet with yellow base, imbricate aestivation, 1.7 cm long, glandular and stellate hairs present on abaxial surface.

Stamen five, polyandrous, epipetalous, heteroanthy has been observed. One anterior anther located below the two dissimilar corolla lobes is larger, recurved and petaloid (1.3 cm long), while remaining four stamens are 1.0 cm long, filament short, basifixed. Dihescence is by apical pore as well as by pores formed at regular intervals in longitudinal suture.

Ovary superior, bicarpellary, syncarpous, bilocular, numerous ovules in each locule with axile placentation, placenta swollen and oblique. Style is long filiform, hairy, stigma bilobed, gynoecium measures 1.8 cm (ovary 2.0 mm; style and stigma 1.6 cm long). Fruit is a berry, changing dark green to blackish brown on ripening.

Solanum citrullifolium

SOLANUM INTEGRIFOLIUM L.

S. integrifolium is wild annual herb, erect 35-60 cm high and spiny with profusely branched tape root. Stem erect, branched herbaceous, cylindrical, solid hairy and spiny. Leaves alternate, petiolate (4.0-7.5 cm long), exstipulate, ovate, 13.9 cm long and 8.4 cm broad, undulate, acute, hairy. Hairs stellate, spines on both sides on vein, unicostate reticulate venation, dark green in colour.

Inflorescence extra axillary cyme, flowers in clusture (2-10). Flowers are pedicellate, ebracteate, complete, bisexual actinomorphic, hypogynous, white in colour.

Calyx with five lobes, occasionally upto seven, gamosepalous, green, inferior 0.5 cm long with stellate hairs and persistent. Corolla with 5 petals, occasionally upto 7, gamopetalous, campanulate, 0.8-1.0 cm long, valvate aestivation, white in colour.

Stamens five, occasionally upto 7, polyandrous, epipetalous, filament short (2.0 mm long), anther 5.0 mm long, yellow, basifixed, dithecous with porous dehiscence.

Ovary superior, bicarpellary, syncarpous, bilocular, numerous ovules with axile placentation, placenta swollen and oblique, style stout, glabrous, stigma 2-3 lobed. Gynoecium measures 1.0 cm. Fruit is a berry, globose, tomato-like changing green to red on ripening.

Solanum integrifolium

SOLANUM KHASIANUM CLARKE

S. khasianum is wild, under shrub or shrub, erect, spiny, 1.0-1.5 meter tall with profusely branched woody root stock. Stem erect, woody, stout much branched, with two types of prickles (straight and distinctly recurved). Leaves simple, 11.5-13.5 cm long, ovate, lobed, lobes lanceolate or triangular, alternate, petiolate, petiole spiny, 5.0-9.0 cm long, lamina with much variation in shape and size, mid rib prominent, prickles on both the surfaces.

Inflorescence is 1-4 flowered cyme. Flowers with spiny pedicel, ebracteate, regular, bisexual, actinomorphic, white in colour.

Calyx with 5 sepals, gamosepalous, hairy, 2.0-2.5 mm long, green in colour. Corolla with 5 petals, gamopetalous, 1.0-2.0 cm long and white in colour.

Androecium consistsof 5 stamens, epipetalous, filaments short (2.0 mm long), anther 1.0-1.2 cm long, basifixed, light yellow with porous dehiscence.

Ovary superior, bicarpellary, syncarpous, bilobed, numerous ovules with axile placentation, placenta swollen and oblique. Style 1.1-1.3 cm long, stigma bilobed, heterostyly present. Fruit is a berry, globose, changing green to yellow on ripening.

Solanum khasianum

SOLANUM SISYMBRIFOLIUM LAM.

S. sisymbrifolium is a perennial under shrub, 1.0-1.5 meter high, with woody root stock. Stem erect, branched, woody, cylindrical, solid hairy, and spiny. Leaves alternate, petiolate, petiole 10-20 cm long, exstipulate, pinnatisect to pinnate compound leaves. Apices of the leaf-let spinous, surface hairy, adaxial surface with stellate hairs while abaxial with stellate and uniseriate hairs, unicostate reticulate venation in leaf-let. Prickles found on mid rib and veins.

Inflorescence extra axillary cyme. Flowers pedicellate, ebracteate, complete, bisexual, actinomorphic, hypogynous, white in colour.

Calyx with five sepals, occasionally 4 or 6, gamosepalous, light green inferior, valvate aestivation, hairy, hairs stellate and glandular, persistent, accrescent and spinous.

Corolla with 5 petals, occasionally 4 or 6, gamopetalous valvate aestivation, campanulate, white, hairy, hairs stellate and glandular. Stamen 5, occasionally 4 or 6, connivent, epipetalous, filament short, basally flattened, basifixed, yellow in colour, anther lobe larger than filament, dithecous with porous dehiscence.

Ovary bicarpellary, syncarpous, superior, bilocular, numerous ovules in each locule, axile placentation, placenta

swollen and oblique. Heterostyly has been observed. Stigma bilobed and prominent. Fruit is a berry globose, cherry-like changing green to deep red on ripening.

Solanum sisymbrifolium

FLORAL ORGANOGENY

Differentiation of floral parts takes place in acropetal succession in *S. aethiopicum*, *S. citrullifolium*, *S. integrifolium*, *S. khasianum* and *S. sisymbrifolium*.

The floral primordium arises as a small rounded mass of cells, which soon becomes broad and somewhat hemispherical at the top (Fig. 1). The calyx originates at an early stage as a small marginal ring having five lobes and in a median longitudinal section the calyx lobes appear as small out growths on each side of the floral axis (Fig. 2). Considerable development of calyx takes place before the differentiation of other floral structures. The corolla lobes arise as a small protuberances (Fig. 3). The corolla is slightly thinner than the calyx, its growth is less upright and margins in-curved (Fig. 4). After the initiation of corolla lobes the stamen primordia arise as upright lobes from the margin of the receptacle (Fig. 4). During further growth the stamen primordium differentiates into a bulbous apex and a narrow basal part (Fig. 5), which differentiate as anther and filament respectively. Later, the anther becomes bilobed. The floral apex left after the differentiation of androecium is utilized in the formation of gynoecium. The ovary wall arises as a circular ring of tissue within the circle of stamen (Fig. 6). Soon the growth begins in the central part of the receptacle forming the placenta, which grows upward slowly than the wall of the carpel (Figs. 6,7). The ovary wall

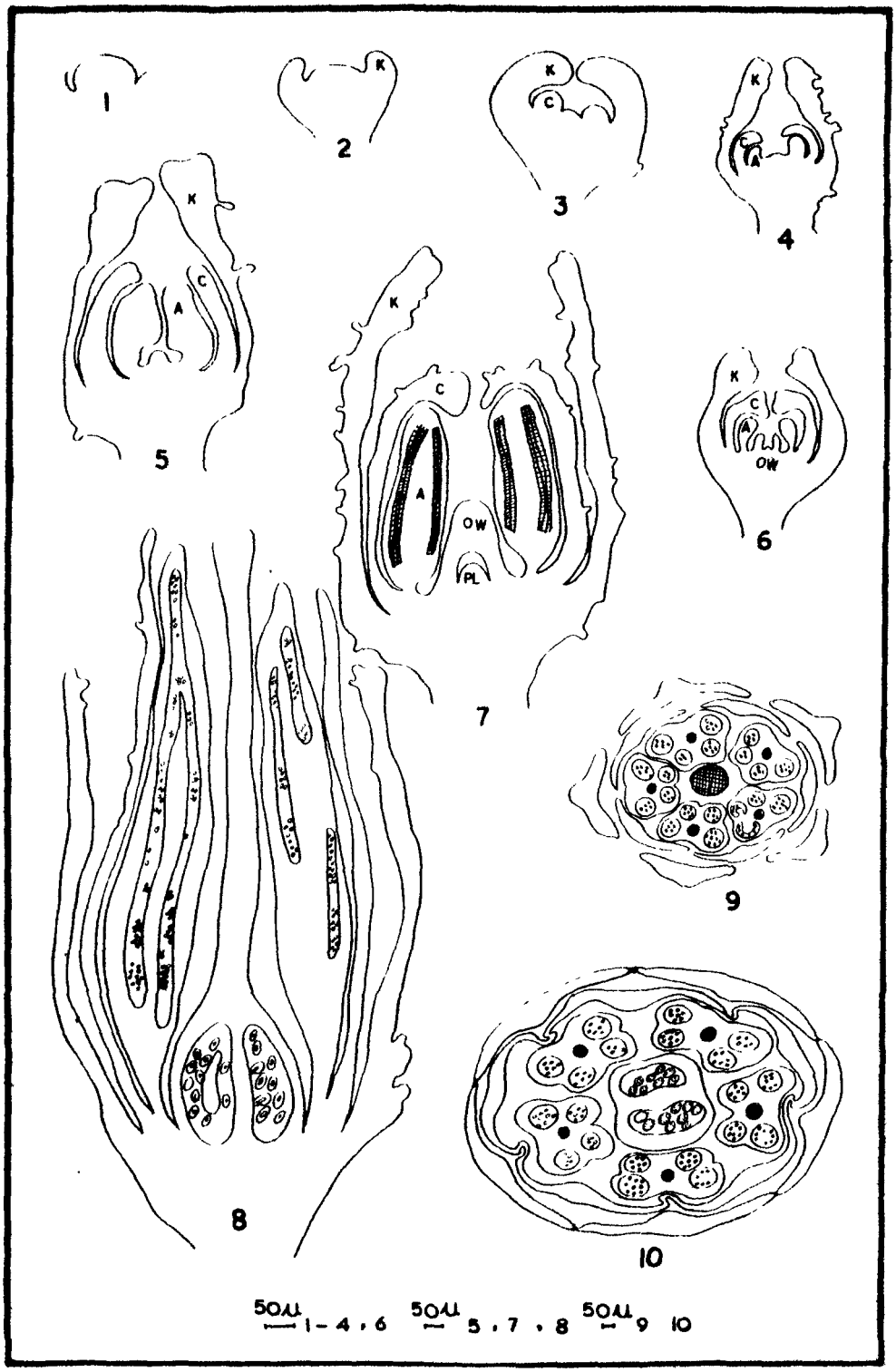
covers the placenta completely, straightens and forms a long style (Figs. 7,8).

A transverse section of well developed flower bud shows five marginal calyx lobes with fused ends (Fig. 10). Inner to calyx ring, the five corolla lobes alternate with the calyx lobes. The corolla lobes are thin, rolled inward and their ends are fused (Fig. 10). The five stamens alternate with corolla lobes (Figs. 9,10). The ovary is nearly round and consistsof two carpels (Fig. 10). The ovules develop on the entire surface of placenta in basipetal succession. The style is solid in S. aethiopicum, S. integrifolium and S. khasianum and hollow upto a considerable length in S. citrullifolium and S. sisymbrifolium.

Explanation of figures

Figs.1–10. *Solanum sisymbrifolium*. Floral organogeny. Fig.1. L.s. floral primordium. Fig.2. L.s. young bud showing calyx primordia. Fig.3. L.s. bud showing initiation of corolla primordia. Fig.4. L.s. bud showing initiation of androecium. Fig.5. L.s. bud showing differentiation of anther and filament. Fig.6. L.s. bud showing initiation of ovary wall. Fig.7. L.s. bud showing calyx, corolla, stamens and initiation of placenta. Fig.8. L.s. mature flower bud. Fig.9. T.s. of bud passing through anthers and style. Fig.10. T.s. flower bud passing through ovary.

(K = calyx; C = corolla; A = androecium; OW = ovary wall; Pl = placenta).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MICROSPORANGIUM

The anther primordium differentiates as a bulbous out growth at the tip of the young stamen. Soon it becomes bilobed and each lobe bears two loculi.

The young anther is quadrangular in transection and composed of homogeneous mass of cells bounded by a well defined epidermis. Soon the hypodermal male archesporium differentiates at the four corners of the young anther, thus the anthers become four chambered (Figs.11,22,34,46,56). The archesporial cells possess dense cytoplasm and prominent nuclei (Figs.12,23,35,47, 57). The archesporial cells divide periclinally producing a primary parietal layer towards epidermis and a sporogenous layer towards the inner side (Figs.13,24,36,47,48,58). The cells of the sporogenous layer divide mitotically forming a large number of sporogenous cells, which differentiate as microspore mother cells. The cells of primary parietal layer divide periclinally forming an outer and an inner secondary parietal layers (Figs. 13,14,25,36,48,49,58,59). In *S. aethiopicum*, *S. citrullifolium*, *S. integrifolium* and *S. sisymbrifolium* the outer secondary parietal layer divides periclinally producing two layers of cells (Figs.14,15,25,26,37,38,59,60), of which the outer layer differentiates as endothecium and inner as middle layer. The inner secondary parietal layer directly differentiates as tapetum (Figs.15,26,38,39,60,61). The middle layer is contributed by the outer secondary parietal layer. Thus the development of

anther wall layers conforms to the Dicotyledonous type. In S. citrullifolium the development of anther wall layers in the petaloid anther resembles that in normal anthers.

In S. khasianum the outer secondary parietal layer divides periclinally producing two layers (Figs.49,51). The outer one differentiates as endothecium and inner as middle layer. The inner secondary parietal layer also divides in the similar plane producing two layers (Figs.50,51), of which the inner layer differentiates as tapetum and the outer as middle layer. The middle layers are contributed by both the secondary parietal layers. Thus the anther wall development in S. khasianum corresponds to the Basic type.

Epidermal cells in fully developed anthers are almost isodiametric in S. aethiopicum, S. citrullifolium and S. sisymbrifolium, (Figs.16,17,27,29,66), radially elongated in S. integrifolium (Fig. 40) and tangentially flattened in S. khasianum (Fig. 53). At the tip region the epidermal cells are tangentially flattened in all the species described here (Figs. 19,31,45,55,65). The epidermal cells possess vacuolated cytoplasm.

The endothecium is 1–3 layered in S. aethiopicum (Figs.16–18), 2–3 layered in S. citrullifolium, S. khasianum and S. sisymbrifolium (Figs.27,29,30,52,54,61,62,64) and 3–4 layered in S. integrifolium (Fig. 40). Endothecium is devoid of fibrous thickenings except at the tip region (Figs.19,31, 45,55,65).

Next to the endothecium are middle layers, which are in the form of narrow strips of cells. Middle layers are 1-2 layered in S. aethiopicum, S. citrullifolium (Figs.16,17,27,29), 2-layered in S. integrifolium and S. khasianum (Figs.40,52,53) and 1-3 layered in S. sisymbrifolium (Figs.61,62,66). During the maturation of pollen grains the middle layers are crushed and absorbed.

Tapetum is of dual origin. One which develops from the innermost derivative of parietal tissue and other towards the connective side. The tapetal cells are radially elongated in S. aethiopicum, S. citrullifolium and S. integrifolium (Figs.16,17,27,40), while it is tangentially elongated in S. khasianum and S. sisymbrifolium (Figs.52,53,62). Tapetum is generally single layered. Exceptionally in S. sisymbrifolium it becomes two layered at places (Fig. 66). The tapetal cells are 1-2 nucleate in S. aethiopicum, S. khasianum and S. sisymbrifolium (Figs.16,17,53,61,62,66), 1-4 nucleate in S. citrullifolium (Figs. 27,28) and upto 6-nucleate in S. integrifolium (Figs.40-43). The tapetal cells possess dense cytoplasm in S. khasianum and S. sisymbrifolium (Figs.53,62,63,66), and vacuolated cytoplasm in S. aethiopicum, S. citrullifolium and S. integrifolium (Figs.16,17,27,28,40-43). The cells of tapetum in S. sisymbrifolium are filled with Ubish granules (Figs.62,63, 66). During the further maturation of anther these granules develop in all the persistent wall layers (Fig. 64). The tapetum is absorbed during the maturation of pollen grains. Thus the

dehisced anther comprises only the epidermis and layers of endothecium (Figs.18,21,30,33,44,54,64).

The dehiscence of the anther is by apical pore in S. integrifolium, S. khasianum and S. sisymbrifolium, while in S. aethiopicum and S. citrullifolium it is by apical pore as well as by pores formed at regular intervals in longitudinal suture. In S. aethiopicum and S. citrullifolium some hypodermal cells of septal region between the two pollen sacs differentiate into resorption tissue. During further development, the cell walls and the protoplast of these cells degenerate and a lysigenous cavity is formed. The process of lysis continues till the adjacent parenchyma is consumed and a passage between the two pollen sacs is formed (Figs.20,32). The resorption passage broadens and a stomium is differentiated in the epidermis opposite to the resorption passage (Figs.21,33). The cells of stomium soon disjoin forming a perforation.

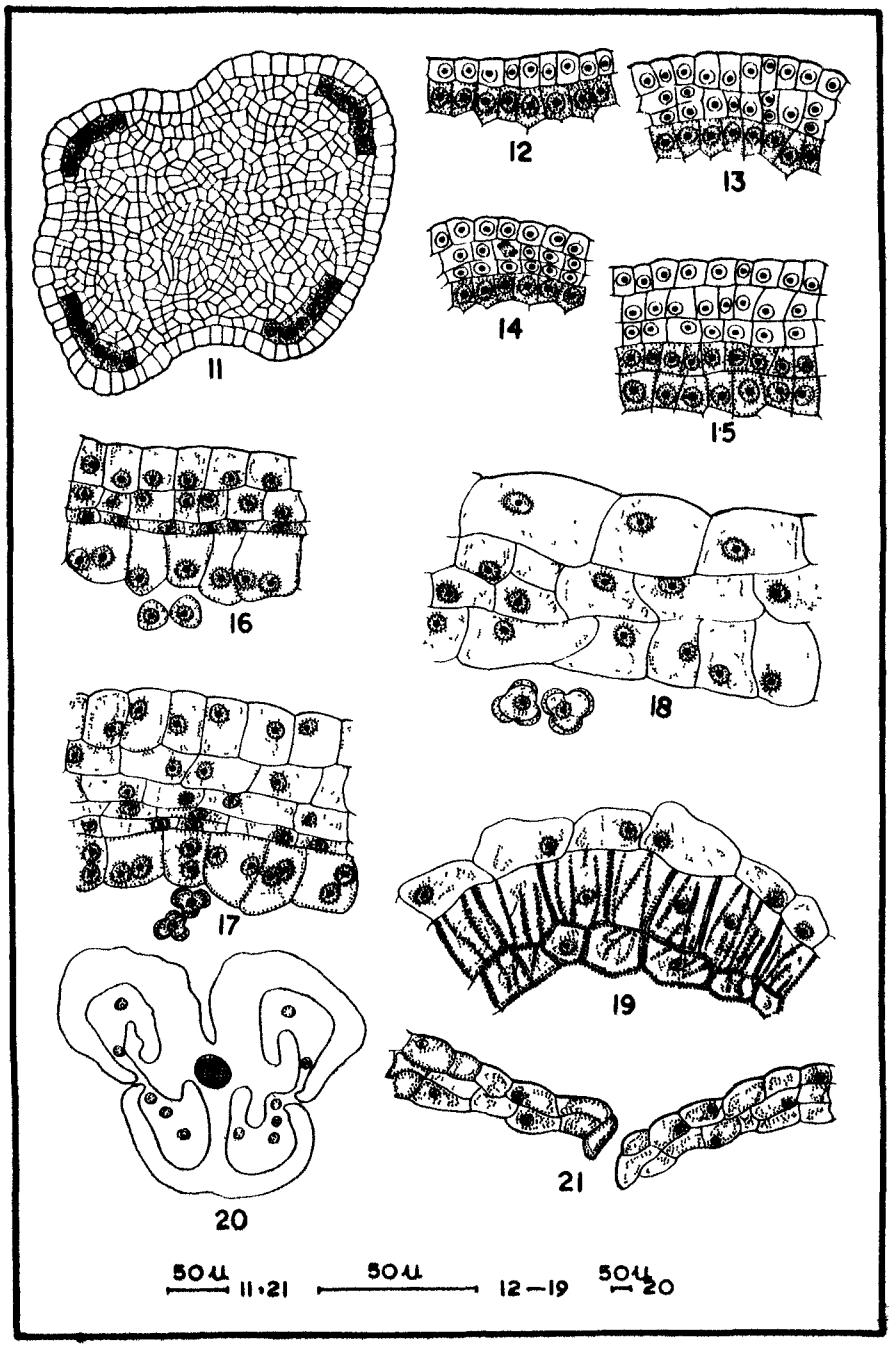
MICROSPORANGIUM

DISTINGUISHING CHARACTERS

Characters	S. aethiopicum	S. citrullifolium	S. integrifolium	S. khasianum	S. sisymbrifolium
Microsporangium	4-chambered	4-chambered	4-chambered	4-chambered	4-chambered
Anther wall development	Dicotyledonous	Dicotyledonous	Dicotyledonous	Basic	Dicotyledonous
Epidermis	Isodiametric cells	Isodiametric cells	Radially elongated cells	Tangentially flattened cells	Isodiametric cells
Endothecium	1-2 layered fibrous thickenings only at tip region	2-layered occasionally 3-layered fibrous thickenings only at tip region	4-layered occasionally 3-layered fibrous thickenings only at tip region	2-layered occasionally 3-layered fibrous thickenings only at tip region	3-layered fibrous thickening only at tip region
Middle layers	Usually one occasionally two	Usually two occasionally one	2-layers	2-layers	2-layers occasionally one and three
Tapetum	Single layered 1-2 nucleate cells	Single layered 1-4 nucleate cells	Single layered 1-6 nucleate cells	Single layered 1-2 nucleate cells	Single layered occasionally 2-layered at places 1-2 nucleate cells
Dehiscence	Porous as well as by pores formed in longitudinal suture	Porous as well as by pores formed in longitudinal suture	Porous	Porous	Porous

Explanation of figures

Figs.11-21. *S. aethiopicum*. Microsporangium. Fig.11. T.s. young anther showing male archesporium at the four corners. Fig.12. L.s. part anther showing hypodermal male archesporium. Fig.13. L.s. part anther showing sporogenous and primary parietal layer; some cells of primary parietal layer have divided periclinally. Fig.14. L.s. part anther showing division in the outer secondary parietal layer. Fig.15. L.s. part anther showing initials of endothecium, middle layer, tapetum and sporogenous layer. Figs.16,17. T.s. part anthers showing epidermis, 1-2-layered endothecium, 1-2 middle layers, 1-2-nucleate tapetum and microspores. Fig.18. L.s. part dehisced anther showing epidermis and persistent 2-3-layered endothecium. Fig.19. L.s. part anther through tip region showing fibrous endothecium. Fig.20. T.s. dehisced anther showing resorption passage. Fig.21. T.s. part anther through pore in longitudinal suture.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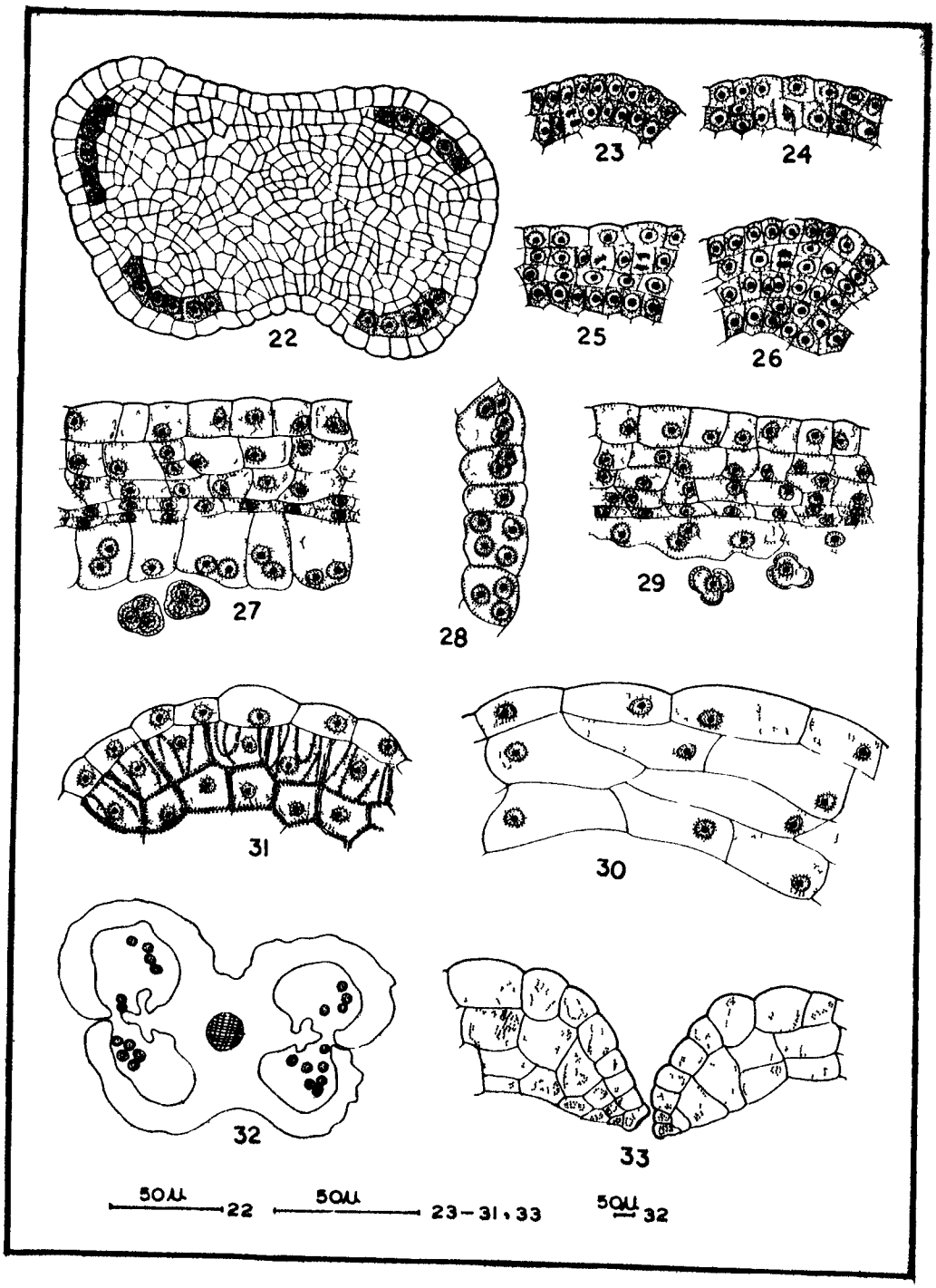
Explanation of figures

Figs.22-33. *S. citrullifolium*. Microsporangium. Fig.22. T.s. of young anther showing male archesprium at four corners. Figs.23,24. L.s. part of young anthers showing division in the hypodermal male archesporium. Figs.25,26. L.s. part of young anthers showing division in outer secondary parietal layer and differentiation of tapetum and sporogenous layer. Fig.27. L.s. part of anther showing structural details of anther wall layers; Note 2-3-layered endothecium and middle layers. Fig.28. 1-4-nucleate tapetum. Fig.29. T.s. anther showing degeneration of tapetum. Fig.30. T.s. part of dehisced anther showing epidermis and 2-3-layered persistent nonfibrous endothecium. Fig.31. L.s. part of anther through tip region showing fibrous endothecium. Fig.32. T.s. dehisced anther showing resorption passage and pore in longitudinal suture. Fig.33. T.s. part of anther passing through pore in longitudinal suture.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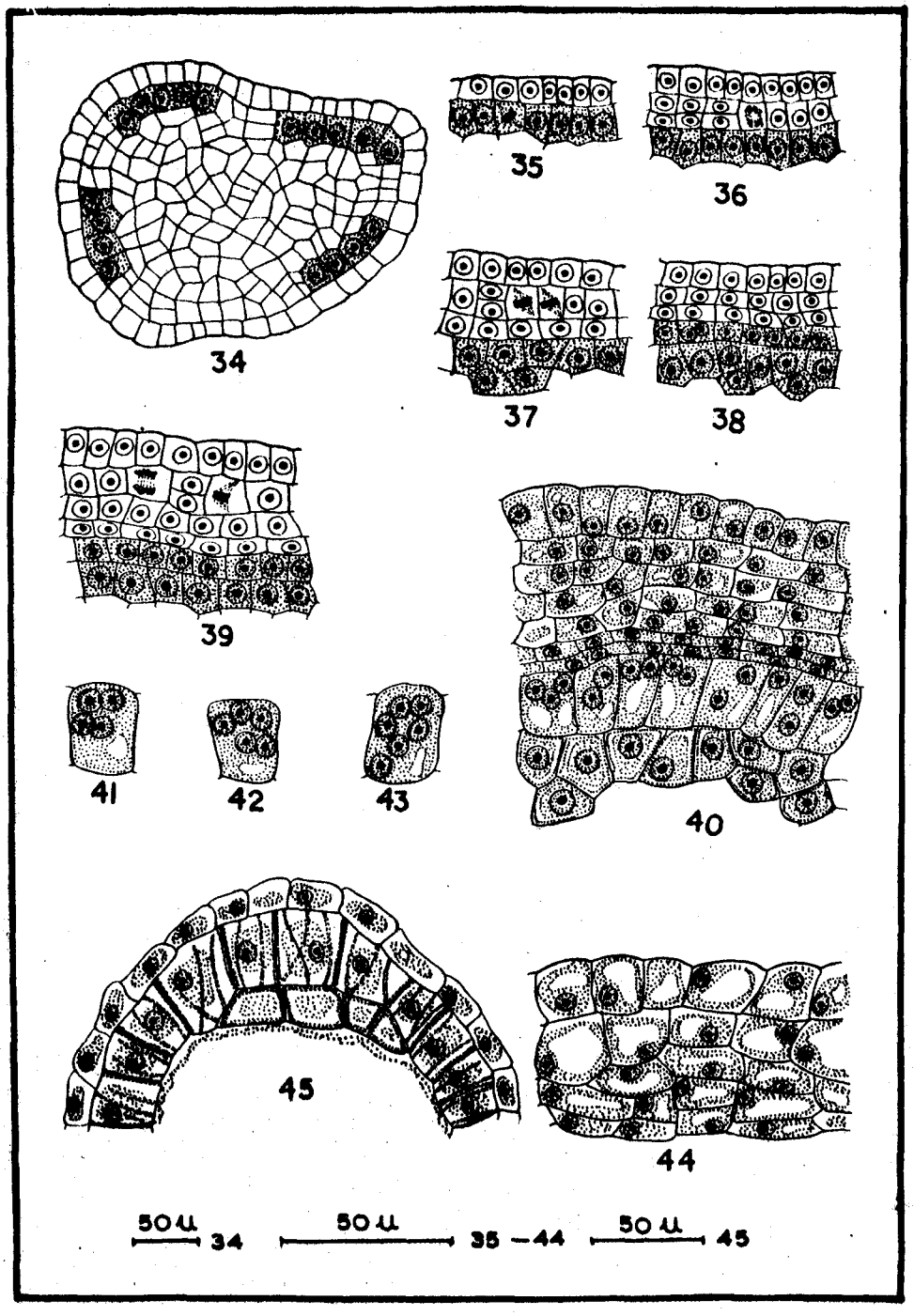
Explanation of figures

Figs.34–45. *S. integrifolium*. Microsporangium. Fig.34. T.s. of young anther showing male archesporium at the four corners. Fig.35. L.s. part young anther showing division in male archesporium. Fig.36. L.s. part of anther showing division in primary parietal layer. Fig.37. L.s. part of anther showing division in outer secondary parietal layer. Fig.38. L.s. part anther showing differentiation of tapetum, initials of endothecium and middle layer. Fig.39. L.s. part of anther showing division in initials of endothecium. Fig.40. L.s. part of anther showing structural details of anther wall layers. Figs.41–43. 4–6-nucleate tapetal cells respectively. Fig.44. L.s. part of dehisced anther showing epidermis and 3–4-layers of persistent nonfibrous endothecium. Fig.45. L.s. part of anther through tip region showing fibrous endothecium.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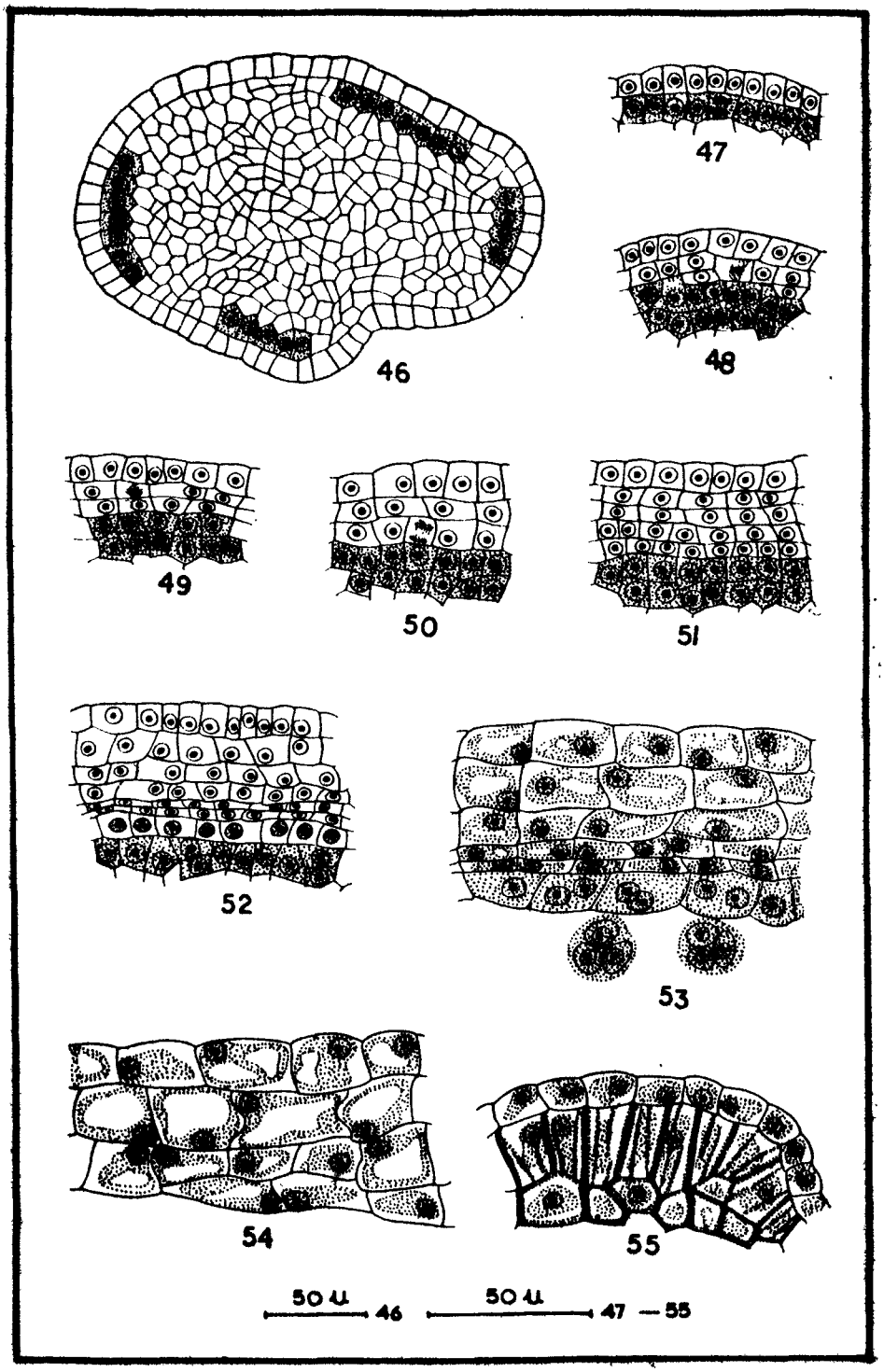
Explanation of figures

Figs.46-55. *S. khasianum*. Microsporangium. Fig.46. T.s. of young anther showing male archesporium at four corners. Fig.47. L.s. part of anther showing division in hypodermal male archesporium. Fig.48. L.s. part of anther showing division in primary parietal layer. Figs.49,50. L.s. part of anthers showing division in outer and inner secondary parietal layers respectively. Fig.51. L.s. part of anther showing initials of endothecium, 2-middle layers, tapetum and sporogenous tissue. Fig.52. L.s. part of anther showing 3-layered endothecium, 2-middle layers, tapetum and sporogenous tissue. Fig.53. L.s. part of anther showing structural details of anther wall layers. Fig.54. L.s. part of dehisced anther showing epidermis and persistent 2-3-layered endothecium. Fig.55. L.s. part of anther through tip region showing fibrous endothecium.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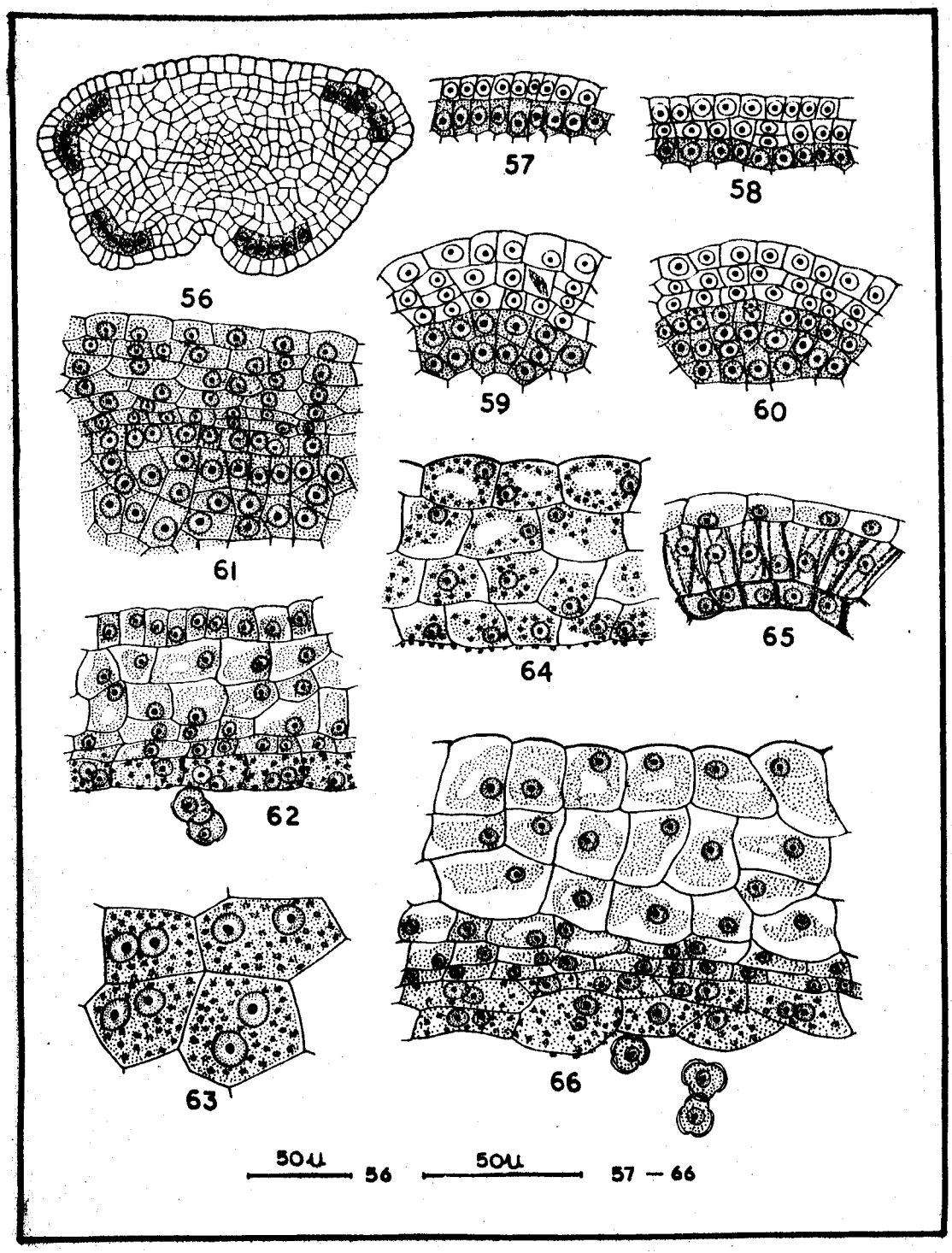
Explanation of figures

Figs.56–66. *S. nisymbrifolium*. Microsporangium. Fig.56. T.s. of young anther showing male archesporium at four corners. Fig.57. L.s. part of anther showing hypodermal male archesporium. Fig.58. L.s. part of anther showing primary parietal layer and sporogenous layer. Fig.59. L.s. part of anther showing division in outer secondary parietal layer, inner secondary parietal layer and sporogenous tissue. Fig.60. L.s. part of anther showing differentiation of tapetum, initials of endothecium and middle layer. Figs.61,62. L.s. part of anther showing structural details; Note Ubish granules in fig.62. Fig.63. Surface view of 2-nucleate tapetal cells showing Ubish granules. Fig.64. L.s. part of dehisced anther showing epidermis and persistent 3-layered endothecium with Ubish granules. Fig.65. L.s. anther through tip region showing fibrous endothecium. Fig.66. L.s. part of anther showing 2-layered tapetum.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MICROSPOROGENESIS

Prior to the initiation of meiosis in the microspore mother cells a mucilaginous layer of considerable thickness is deposited within the original wall.

The microspore mother cells undergo meiosis and produce microspore tetrads. The divisions in all the microspore mother cells of an anther may not be synchronous. Thus different divisional stages of microsporogenesis may be present in the four chambers of the same anther (Figs.67-74,83-94,107-115,126-137, 148-159). Cell plate is not laid down after meiosis I and the spindle fibers remain during the meiosis II. The cell plate is laid down after meiosis II when the spindle fibers disappear, so the cytokinesis is of simultaneous type.

Chromosomal abnormalities at meiosis I and II have been observed in S. aethiopicum, S. citrullifolium, S. integrifolium, S. khasianum and S. sisymbrifolium. Early separation of chromosomes occur in S. citrullifolium and S. sisymbrifolium (Figs.90,133). Laggards are more frequent in S. citrullifolium, S. integrifolium, S. khasianum and S. sisymbrifolium (Figs.91, 92,114,115,134-136,155-157). Whereas unequal separation with 4 and 20 and 8 and 16 chromosomes at anaphase I has been observed in S. citrullifolium and S. sisymbrifolium respectively (Figs.94,158). Besides, disorientation of chromosomes forming three groups may occasionally occur in S. khasianum and S. sisymbrifolium (Figs.137,159). The orientation of spindles at

metaphase II is variable, thus different types of microspore tetrads are formed. The microspore tetrads are generally tetrahedral (Figs.75,95,116,138,160), occasionally decussate (Figs. 76,96,117,139,161), rarely isobilateral in S. aethiopicum, S. citrullifolium, S. khasianum and S. sisymbrifolium (Figs.77,97, 118,141,163) and rhomboidal in S. khasianum and S. sisymbrifolium (Figs.140,162). In S. citrullifolium in about 5-10% cases one or some-times two microspores in a microspore tetrad may be deformed (Figs.98,99) because of abnormal behaviour of chromosomes during meiosis.

The microspores develop their own wall although they continue to lie for some time within the original wall.

MALE GAMETOPHYTE

Microspore represents the beginning of the male gametophyte. The wall of microspore mother cell breaks down and the young microspores are liberated in the anther locule. The young microspore is somewhat triangular in outline and thin walled with dense cytoplasm (Figs.78,100,119,142,164). Later, the microspore becomes spherical, increases in size, possesses vacuolated cytoplasm and considerably thick and smooth transparent exine.

Pollen grains are generally tricolporate in S. aethiopicum, S. citrullifolium, S. integrifolium, S. khasianum and S. sisymbrifolium (Figs.79-82, 101-103,120-123,143-147,165-167). During further development of male gametophyte the vacuoles disappear and the cytoplasm becomes dense (Figs.80-82, 101-103,121-125,144-147,166,167). Sometimes the cytoplasm becomes replete with starch grains in S. khasianum (Fig. 144). The division in the microspore nucleus results in a large vegetative and a small generative cell which is delimited by a hyaline wall (Figs.80,121,145,166). Later, the generative cell is detached, rounds up and comes to lie in the cytoplasm of pollen grain (Figs.81,102,122,146,167). In S. aethiopicum and S. integrifolium the generative nucleus divides mitotically and the pollen grains become 3-nucleate (Figs.82,123). The cytoplasm which surrounds the two male gametes is somewhat different

from the general cytoplasm. Thus it appears that two male cells are formed.

Variations in the structure of pollen grains and behaviour of nuclei have also been observed in S. citrullifolium, S. integrifolium and S. khasianum. Occasionally the pollen grains may be bicolporate and multicolporate in S. integrifolium (Figs.124,125). Sometimes in S. citrullifolium and S. khasianum the two nuclei of the pollen grains are of equal size and probably they may give rise to two gametophyte (Figs.103,147).

The germination of pollen grains is monosiphonous. Occasionally polysiphonous condition has also been observed in S. citrullifolium (Fig. 104). Occasionally in situ germination of pollen grains with variable length of pollen tubes has been observed in S. citrullifolium (Figs.105,106).

In S. citrullifolium, S. khasianum and S. sisymbrifolium the pollen grains are shed at 2-nucleate stage (Figs. 102,146,167), whereas in S. aethiopicum and S. integrifolium they are shed at 3-nucleate stage (Figs.82,123).

A great variability in the viability of pollen grains has been observed. It is minimum (24.58%) in S. aethiopicum and maximum (92.44%) in S. khasianum. In S. sisymbrifolium and S. integrifolium viability of pollen grains is 39.41% and 87.46% respectively. In S. citrullifolium the

viability in the normal anther is 66.33% whereas in petaloid anther it is 90.18%. Thus it may be concluded that the sterility is maximum in S. aethiopicum (75.42%) and minimum in S. khasianum (7.66%).

The average diameter of twenty pollen grains measured in S. aethiopicum, S. citrullifolium, S. integrifolium, S. khasianum and S. sisymbrifolium is 20.45 μ, 21.86 μ, 16.87 μ, and 19.05 μ respectively.

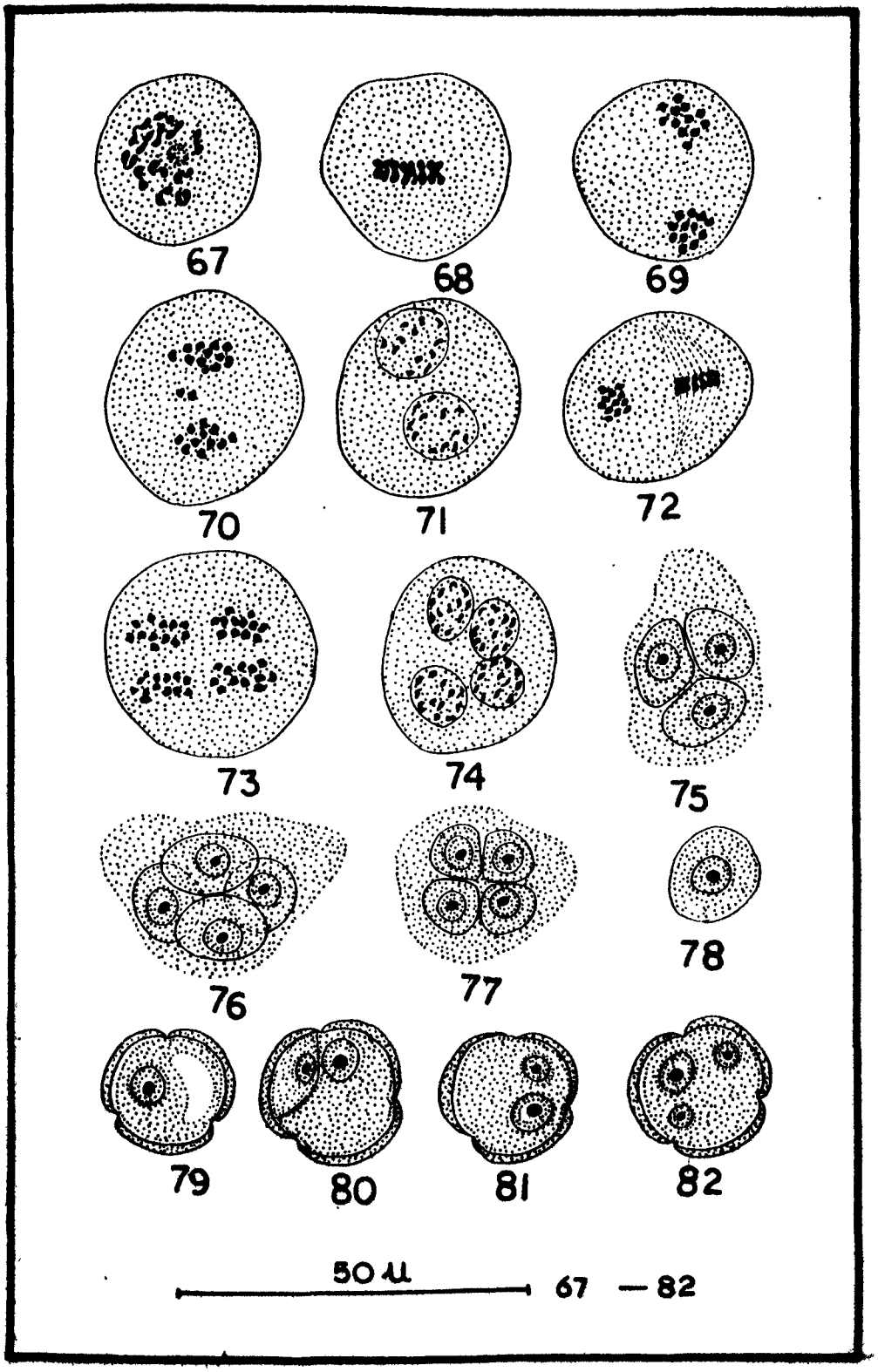
MICROSPOROGENESIS AND MALE GAMETOPHYTE

DISTINGUISHING CHARACTERS

Characters	S. arthingtonum	S. citrullifolium	S. integrifolium	S. khasianum	S. sisymbrifolium
Meiotic division	Non-synchronous	Non-synchronous	Non-synchronous	Non-synchronous	Non-synchronous
Cytokinesis	Simultaneous	Simultaneous	Simultaneous	Simultaneous	Simultaneous
Microspore tetrad	Tetrahedral occasionally decussate, rarely isobilateral	Tetrahedral occasionally decussate, rarely isobilateral	Tetrahedral occasionally decussate, rarely isobilateral	Tetrahedral occasionally decussate, rhomboidal, rarely isobilateral	Tetrahedral occasionally decussate, rhomboidal, rarely isobilateral
Pollen grain	Tricolporate smooth exine	Tricolporate smooth exine	Tricolporate occasionally bi- and multi-colporate smooth exine	Tricolporate occasionally starch grain present smooth exine	Tricolporate smooth exine
Shedding stage	3-nucleate	2-nucleate	3-nucleate	2-nucleate	2-nucleate
Pollen viability	24.58%	66.33%, 90.18% in petaloid anther	87.46%	92.44%	39.41%
Size of pollen grain	20.45 μ	21.86 μ	16.89 μ	22.8 μ	19.05 μ
Pollen germination	Monosiphonous	Mono and polysiphonous *in situ* germination	Monosiphonous	Monosiphonous	Monosiphonous

Explanation of figures

Figs.67-82. *S. aethiopicum*. Microsporogenesis and male gametophyte. Figs.67-74. Microspore mother cells undergoing meiosis. Figs.75-77. Tetrahedral, decussate and isobilateral microspore tetrads respectively. Fig.78. Young microspore. Fig.79. Uninucleate pollen grain. Fig.80. Two celled pollen grain showing a large vegetative and a small generative cell. Fig.81. Two nucleate pollen grain. Fig.82. Three nucleate pollen grain.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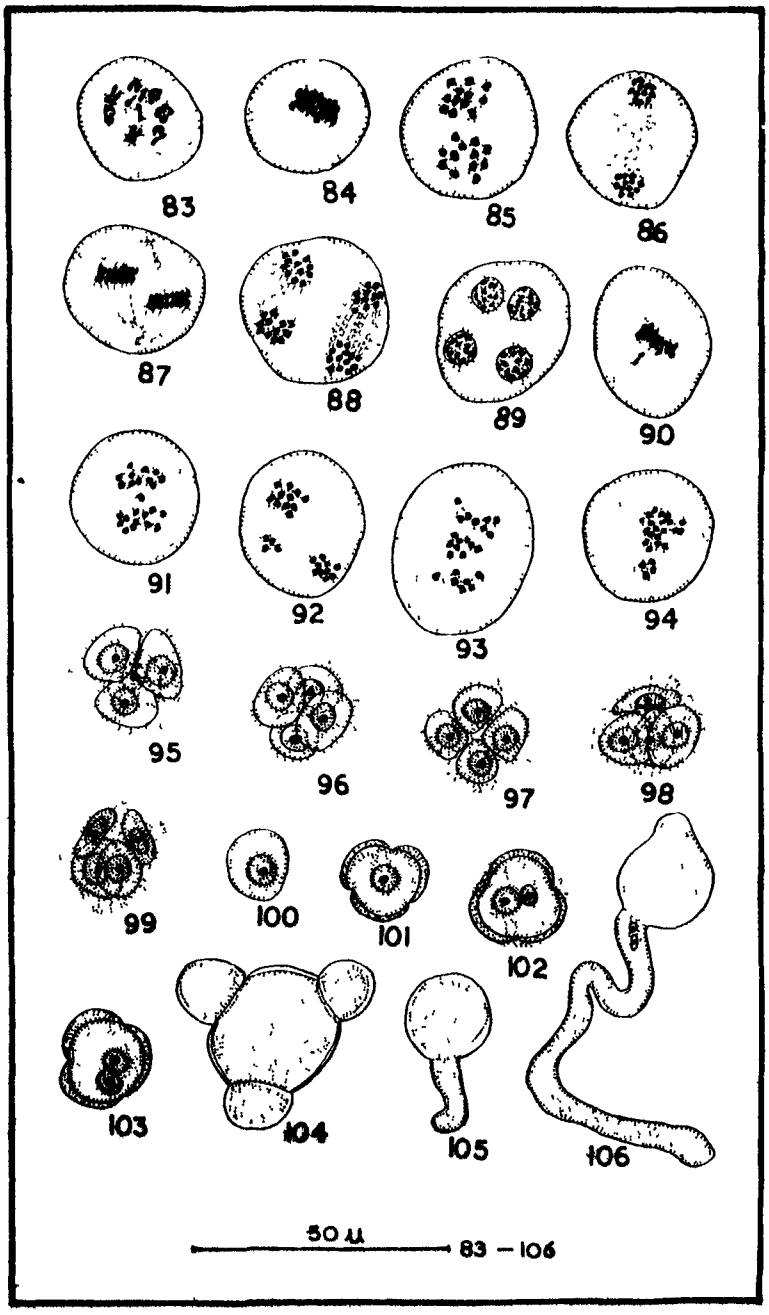
Explanation of figures

Figs.83–106. *S. citrullifolium*. Microsporogenesis and male gametophyte. Figs.83–89. Microspore mother cells undergoing meiosis. Fig.90. Early separation of chromosome at metaphase I. Figs.91,92. Lagging chromosomes at anaphase I. Fig.93. Disorientation of chromosomes forming three groups. Fig.94. Unequal separation of chromosomes at anaphase I. Figs.95–97. Tetrahedral, decussate and isobilateral microspore tetrads respectively. Fig.98. Microspore tetrad with three healthy and one deformed microspores. Fig.99. Microspore tetrad with two healthy and two deformed microspores. Fig.100. Young microspore. Figs.101,102. One and two nucleate pollen grains respectively. Fig.103. Two nucleate pollen grain showing both the nuclei of equal size. Fig.104. Pollen grain showing polysiphenous condition. Figs.105,106. *In situ* germination of pollen grains with variable length of pollen tubes.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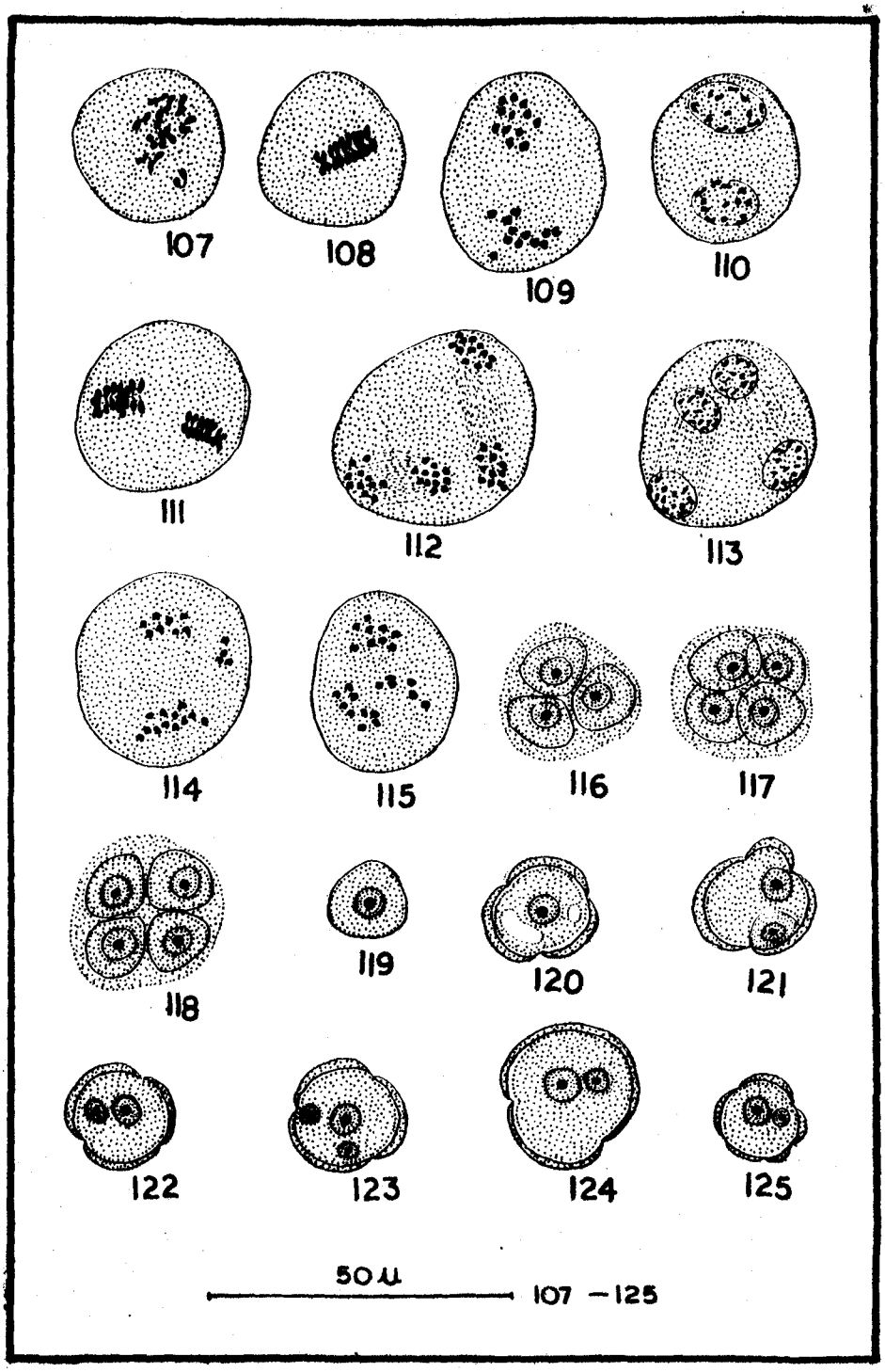
Explanation of figures

Figs.107-125. *S. integrifolium*. Microsporogenesis and male gametophyte. Figs.107-113. Microspore mother cells undergoing meiosis. Figs.114,115. Lagging chromosomes at anaphase I. Figs.116-118. Tetrahedral, decussate and isobilateral microspore tetrads respectively. Fig.119. Young microspore. Fig.120. Uni-nucleate pollen grain with thick exine. Fig.121. Two celled pollen grain showing a large vegetative and a small generative cell. Fig.122. Two nucleate pollen grain. Fig.123. Three nucleate pollen grain. Figs.124,125. Two nucleate bicolporate and multicolporate pollen grains respectively.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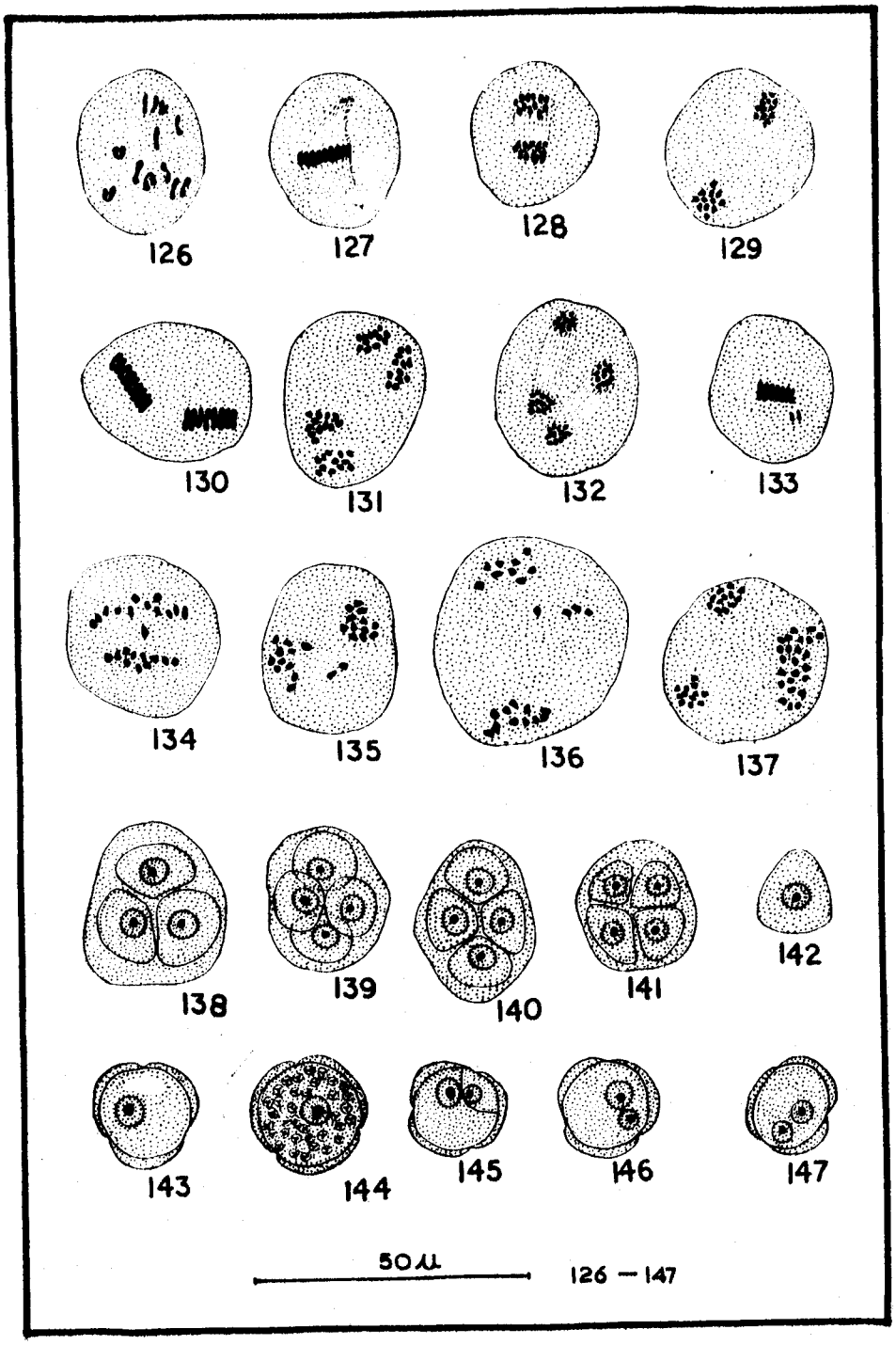
Explanation of figures

Figs.126-147. *S. khasianum*. Microsporogenesis and male gametophyte. Figs.126-132. Microspore mother cells undergoing meiosis. Fig.133. Early separation of chromosomes at metaphase I. Figs.134-136. Lagging chromosomes at anaphase I. Fig.137. Disorientation of chromosomes showing three groups. Figs.138-141. Tetrahedral, decussate, rhomboidal and isobilateral microspore tetrads respectively. Fig.142. Young microspore. Fig.143. Uninucleate pollen grain. Fig.144. Uninucleate pollen grain showing starch grains. Fig.145. Two celled pollen grain showing a large vegetative and a small generative cell. Fig.146. Two-nucleate pollen grain. Fig.147. Two-nucleate pollen grain, both the nuclei are of equal size.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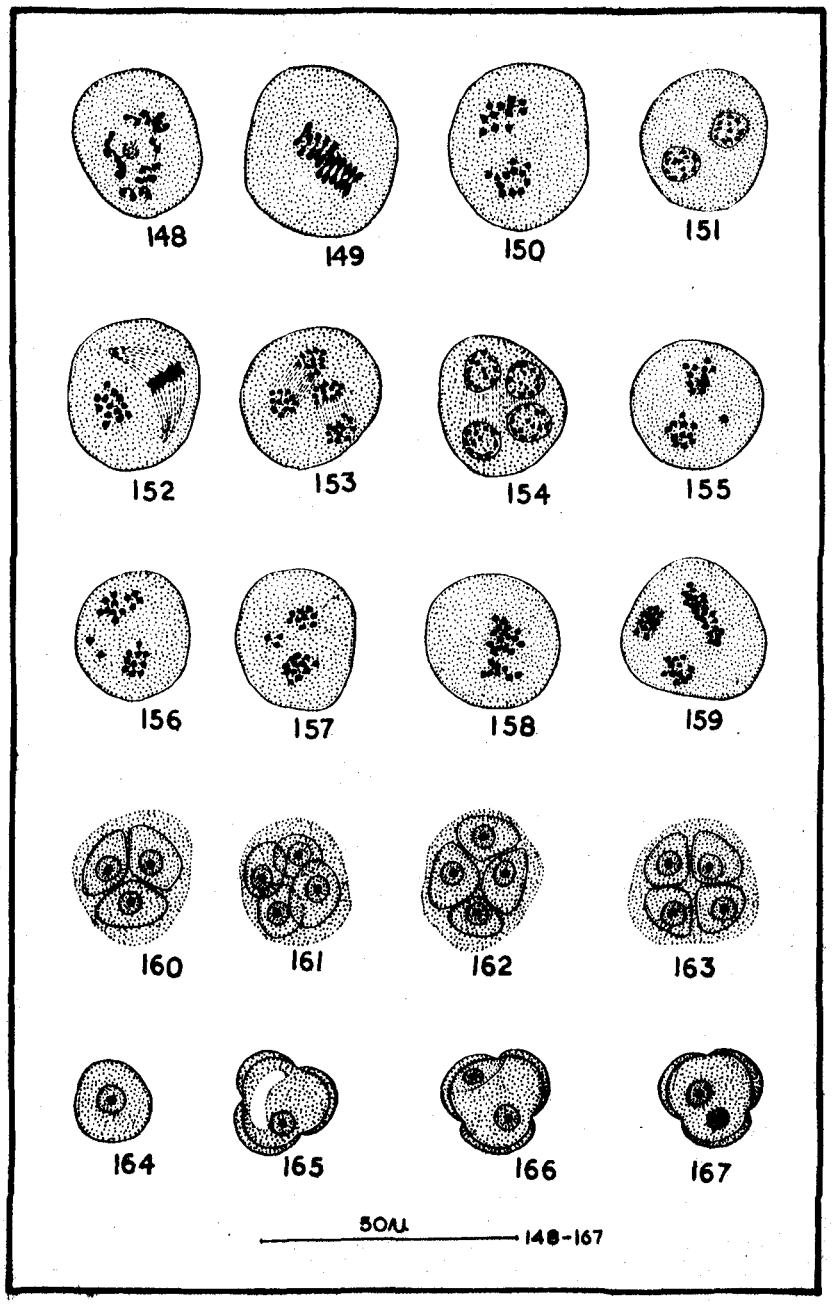
Explanation of figures

Figs.148–167. *S. sisymbrifolium*. Microsporogenesis and male gametophyte. Figs.148–154. Microspore mother cells undergoing meiosis. Figs.155–157. Lagging chromosomes at anaphase I stage of microsporogenesis. Fig.158. Unequal separation of chromosomes at anaphase I. Fig.159. Dis-orientation of chromosomes showing three groups. Figs.160–163. Tetrahedral, decussate, rhomboidal and isobilateral microspore tetrads respectively. Fig.164. Young micro-spore. Fig.165. Uni-nucleate pollen grain with thick exine and vacuolated cytoplasm. Fig.166. Two celled pollen grain showing a large vegetative and a small generative cell. Fig.167. Two nucleate pollen grain.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MEGASPORANGIUM

The ontogeny and structure of ovule in S. aethiopicum, S. citrullifolium, S. integrifolium, S. khasianum and S. sisymbrifolium are more or less same with minor differences.

The young placenta is composed of homogeneous mass of cells. At places the cells of epidermis and 2-3 hypodermal layers become densely cytoplasmic and possess prominent nuclei. The hypodermal cells in these areas begin to divide in all the planes while the epidermal cells covering these areas divide anticlinally. As a result a small protuberance is formed which constitute the ovular primordium (Figs. 176,183,190,198). In S. citrullifolium the ovules situated at the top of placenta face upward while those of middle and bottom region face downward. In S. integrifolium the ovules face upward. In S. aethiopicum, S. khasianum and S. sisymbrifolium the ovules situated in the middle and top of placenta face upward while rest face downward.

The ovules in S. aethiopicum, S. citrullifolium, S. integrifolium, S. khasianum and S. sisymbrifolium essentially conform to anatropous configuration and resemble each other with minor differences. The nucellus is dome-shaped and covers the female archesporial cell (Figs.168,169,177,178,184,191,192,199). It remains single layered through out and remains healthy upto functional megaspore stage in S. integrifolium, S. khasianum and

S. sisymbrifolium (Figs.186,193,201). The nucellus degenerates completely at 2- ucleate embryo sac stage, thus the micropylar part of the sac becomes naked (Figs.172,180,187,194,202). The primordium of integument arises at megaspore mother cell stage in all the five species described here (Figs.169,177,178,185, 191,192,199). The integument grows rapidly and reaches the level of the nucellus before the initiation of meiotic divisions in the megaspore mother cell in S. integrifolium and S. khasianum (Figs.185,192), whereas in S. aethiopicum, S. citrullifolium and S. sisymbrifolium the growth of the integument is comparatively slow (Figs.170,178,200). The integument grows further and forms a narrow micropylar canal at megaspore tetrad stage in S. citrullifolium (Fig.179), and at functional megaspore stage in S. aethiopicum (Fig.171), while in S. khasianum and S. sisymbrifolium the micropyle is short and wide (Figs.193,201). In S. integrifolium the growth of the integument is slow and the micropyle is formed at 2-nucleate embryo sac stage (Fig.187). The micropyle becomes long and narrow during further development of female gametophyte (Figs.172-174,180-182,187-189,194-196,202-204).

In S. aethiopicum, S. citrullifolium and S. integrifolium the ovule starts its curvature at female archesporial cell stage (Figs.168,177,184), whereas in S. khasianum and S. sisymbrifolium the curvature starts at megaspore mother cell stage (Figs.192,199). The curvature of the ovule continues and the ovule becomes almost hemianatropous at functional megaspore

stage in S. aethiopicum, S. integrifolium, S. khasianum and S. sisymbrifolium (Figs.171,186,193,201) and at megaspore tetrad stage in S. citrullifolium (Fig.179). The ovules assume hemi-anatropous configuration at 2-nucleate embryo sac stage in S. integrifolium (Fig.187), while it becomes almost anatropous in S. aethiopicum (Fig.172,173), S. citrullifolium (Figs.180,181), S. khasianum (Figs.194,195) and S. sisymbrifolium (Figs.202, 203). The ovules attain maximum curvature at mature embryo sac stage and assume anatropous configuration. Thus the ovules in all the five species described here are anatropous, unitegmic and tenuinucellate (Figs.174,182,189,196,204).

The integument at megaspore mother cell stage is few layered on the free side while at mature embryo sac stage it becomes 7-9 celled thick in S. aethiopicum and S. citrullifolium (Figs.174,182), 7-8 celled thick in S. integrifolium, S. khasianum and S. sisymbrifolium (Figs.189,196,204).

The innermost layer of the integument which is in contact with the embryo sac differentiates as single layered endothelium at 2-nucleate embryo sac stage in S. citrullifolium, S. integrifolium, S. khasianum and S. sisymbrifolium (Figs.180, 187,194,202), whereas in S. aethiopicum it differentiates at functional megaspore stage (Fig.171). The cells of the endothelium are densely cytoplasmic with prominent nuclei in S. aethiopicum, S. citrullifolium, S. khasianum and S. sisymbrifolium (Figs.171,174,180-182,194-196,202-204). However, the

endothelial cells possess vacuolated cytoplasm in S. integrifolium (Figs.187-189). The endothelium persists upto mature seed stage in S. sisymbrifolium, while in S. aethiopicum, S. citrullifolium, S. integrifolium and S. khasianum it degenerates during seed maturity.

The continuity of endothelium is broken at the chalazal end of the ovule where a group of cells differentiates as hypostase at 2-nucleate embryo sac stage (Figs.172,180,187, 194,202). These cells are compactly arranged, thick walled and persist upto mature embryo sac stage. The hypostase usually disorganise during seed development.

In one case in S. aethiopicum it appears that the growth of the integument on the funicular side is suppressed at megaspore mother cell stage (Fig.175), while the integument on the free side has reached the nucellus.

Sometime orthotropous ovules with long and narrow micropyle may develop in S. khasianum (Fig.197). Such ovules may bend due to lack of space in the ovarian cacity.

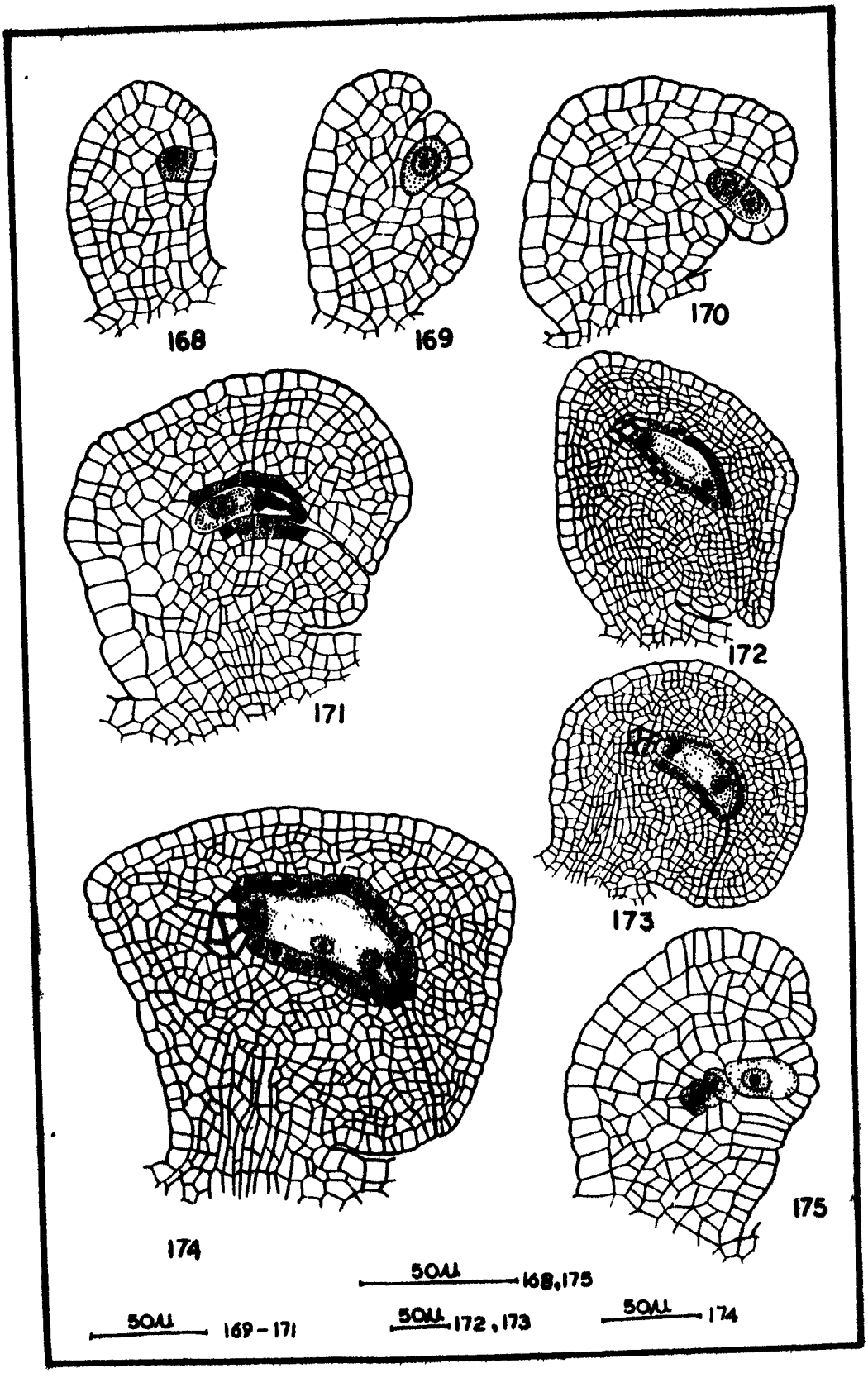
MEGASPORANGIUM

DISTINGUISHING CHARACTERS

Characters	S. asthiense	S. citrullifolium	S. integrifolium	S. khasianum	S. sinuatifolium
Megasporangium	Anatropous, unitegmic and tenuinucellate	Anatropous, unitegmic and tenuinucellate	Anatropous, unitegmic and tenuinucellate	Anatropous, unitegmic and tenuinucellate rarely ortho-tropous	Anatropous, unitegmic and tenuinucellate
Nucellus degenerates at	Functional megaspore	2-nucleate embryo sac	2-nucleate embryo sac	2-nucleate embryo sac	2-nucleate embryo sac
Endothelium differen-tiates at	Functional megaspore	2-nucleate embryo sac	2-nucleate embryo sac	2-nucleate embryo sac	2-nucleate embryo sac
Hypostase develops at	2-nucleate embryo sac	2-nucleate embryo sac	2-nucleate embryo sac	2-nucleate embryo sac	2-nucleate embryo sac
Micropyle is formed at	Functional megaspore	megaspore tetrad stage	2-nucleate embryo sac	Functional megaspore	Dividing functional megaspore
Ovule at 2-nucleate embryo sac stage	Almost anatropous	Almost anatropous	Hemianatropous	Almost anatropous	Almost anatropous
At mature embryo sac stage	Anatropous	Anatropous	Anatropous	Anatropous	Anatropous
Thickness of integument at mature embryo sac stage	7-9 celled	7-9 celled	7-8 celled	7-8 celled	7-8 celled

Explanation of figures

Figs.168-175. *S. aethiopicum*. Development of megasporangium. Fig.168. L.s. of young ovule showing female archesporial cell. Figs.169,170. L.s. of ovules showing the initiation of integument and curvature. Fig.171. L.s. of ovule at functional megaspore stage showing endothelium and micropyle. Figs.172,173. L.s. of ovules at 2 and 4-nucleate embryo sac stage respectively, hypostase has also differentiated. Fig.174. L.s. of mature anatropous ovule at mature embryo sac stage with well differentiated endothelium and hypostase. Fig.175. L.s. of ovule at megaspore mother cell stage showing suppression of integument on funicular side, accessory archesporial cells are also seen below the megaspore mother cell.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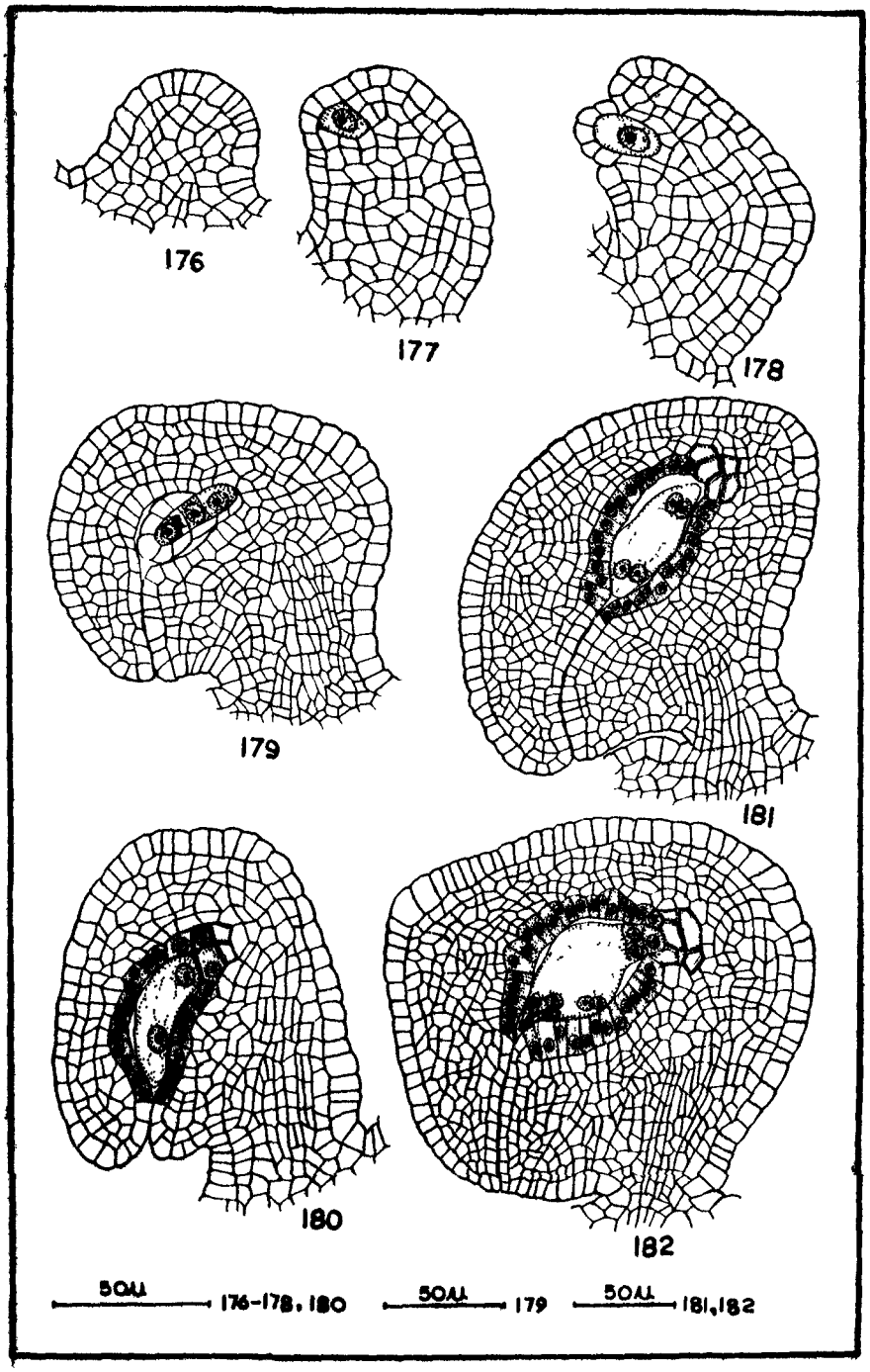
Explanation of figures

Figs.176-182. *S. citrullifolium*. Development of megasporangium. Fig.176. L.s. of ovular primordium. Fig.177. L.s. of young ovule showing initiation of integument and female archesporial cell. Fig.178. L.s. of ovule at megaspore mother cell stage. Fig.179. L.s. of ovule at megaspore tetrad stage showing formation of micropyle and pronounced curvature. Figs.180,181. L.s. of ovules at 2 and 4-nucleate embryo sacs respectively showing endothelium and hypostase. Fig.182. L.s. of mature anatropous ovule at mature embryo sac showing well developed endothelium and hypostase.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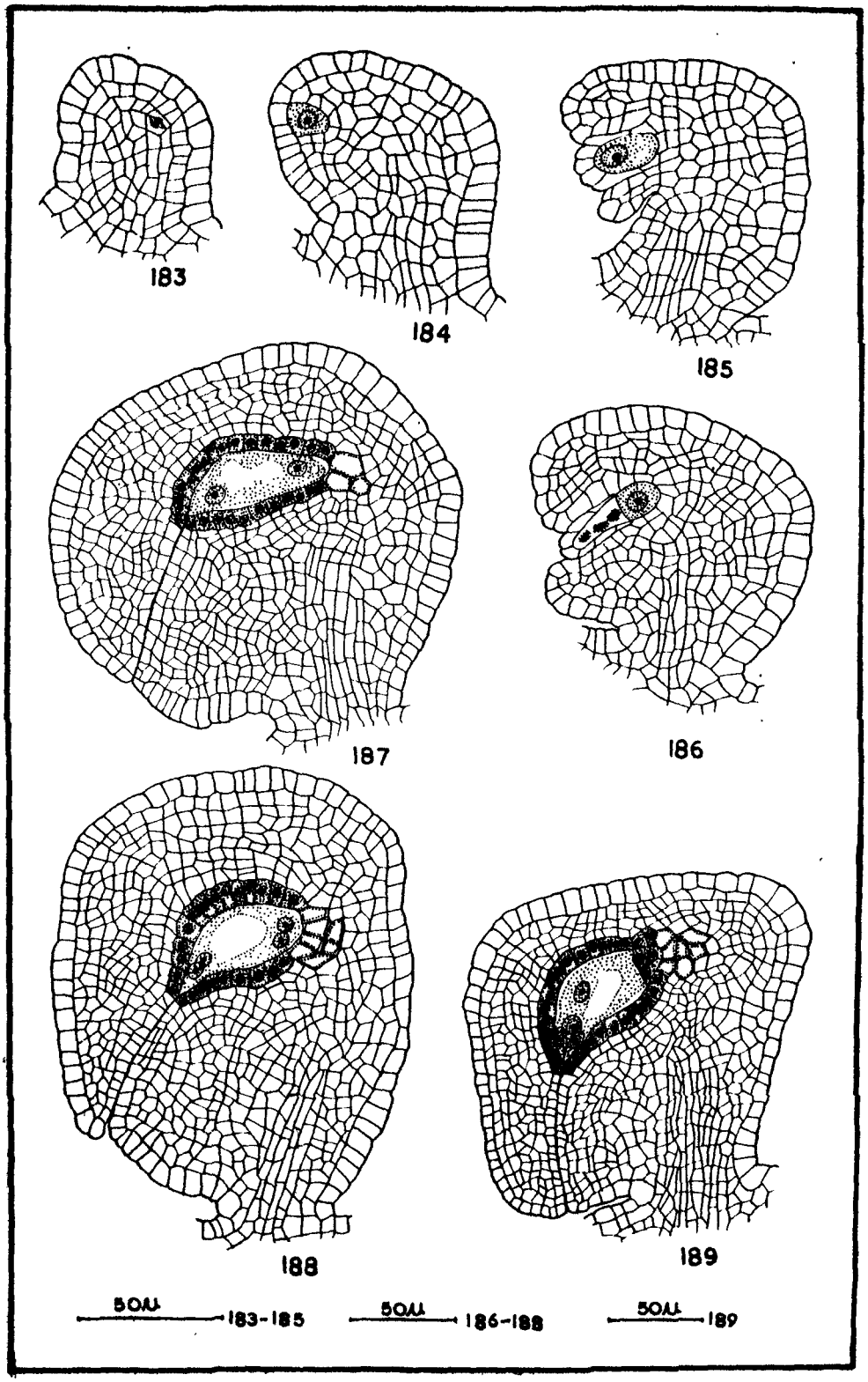
Explanation of figures

Figs.183–189. *S. integrifolium*. Development of megasporangium. Fig.183. L.s. of ovular primordium. Fig.184. L.s. of ovule at archesporial cell stage. Fig.185. L.s. of ovule at megaspore mother cell stage showing initiation of integument. Fig.186. L.s. of ovule at functional megaspore stage. Figs.187,188. L.s. ovules at 2 and 4-nucleate embryo sac stage showing endothelium and hypostase. Fig.189. L.s. of mature anatropous ovule at mature embryo sac stage.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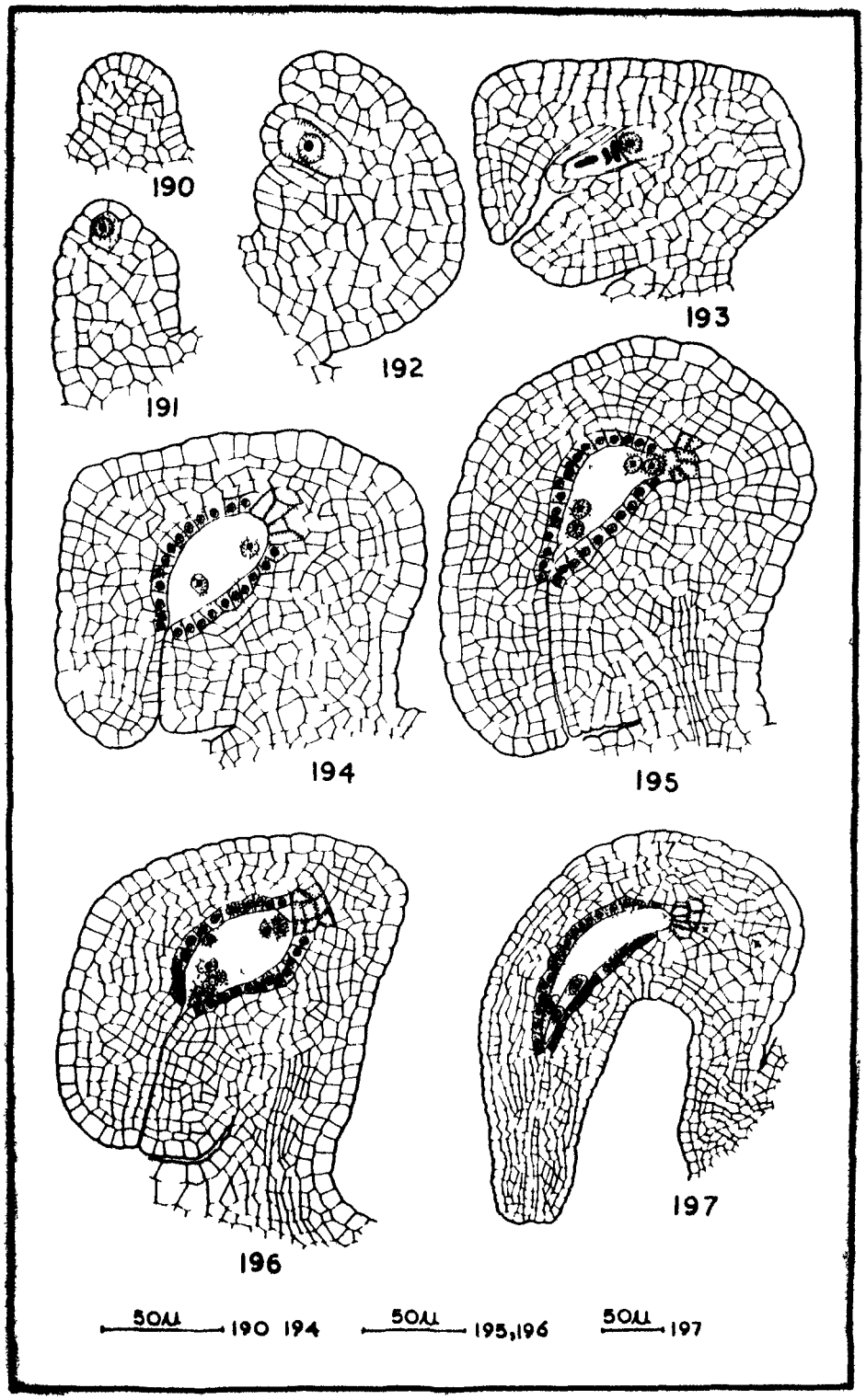
Explanation of figures

Figs.190–197. *S. khasianum*. Development of megasporangium. Fig.190. L.s. of ovular primordium. Fig.191. L.s. of ovule at archesporial cell stage. Fig.192. L.s. of ovule at megaspore mother cell stage showing initiation of integument and curvature. Fig.193. L.s. of ovule at functional megaspore stage, note a short and wide micropyle. Figs.194,195. L.s. ovule at 2 and 4-nucleate embryo sac stage showing endothelium and hypostase. Fig.196. L.s. of mature anatropous ovule at mature embryo sac stage showing well developed endothelium and hypostase. Fig.197. L.s. of an almost orthotropous ovule at mature embryo sac stage with well developed endothelium and hypostase.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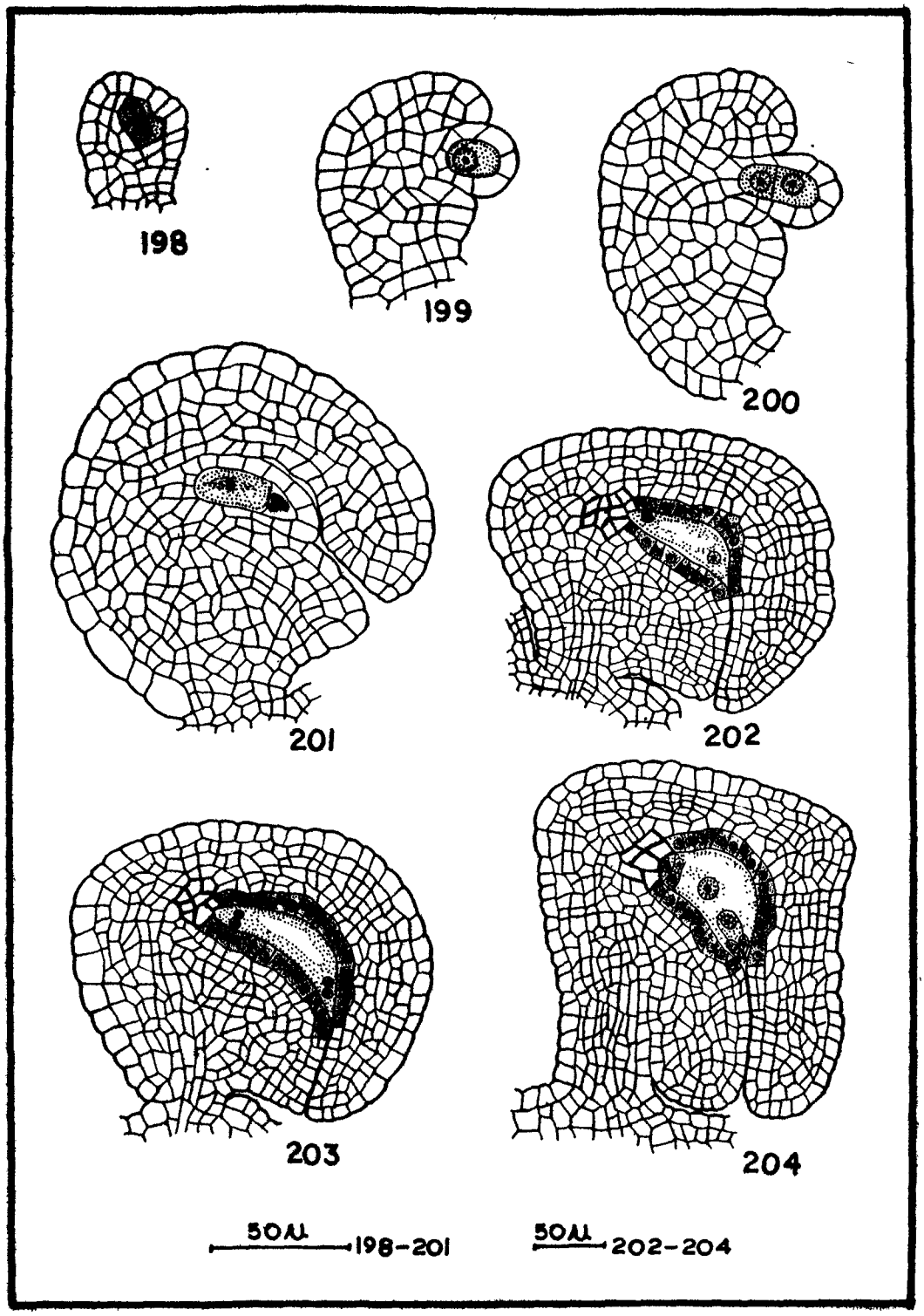
Explanation of figures

Figs.198–204. *S. sisymbrifolium*. Development of megasporangium. Fig.198. L.s. of young ovule at archesporial cell stage. Figs.199,200. L.s. of ovules at megaspore mother cell and dyad stage respectively showing curvature and initiation of integument. Fig.201. L.s. of ovule at functional megaspore stage, the micropyle has formed. Figs.202,203. L.s. of ovules at 2 and 4-nucleate embryo sac stages respectively showing endothelium and hypostase. Fig.204. L.s. of mature anatropous ovule at mature embryo sac stage showing well developed endothelium, a long micropylar canal and hypostase.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MEGASPOROGENESIS

The female archesporium is hypodermal in origin and differentiates at an early stage of ovule development. It possesses dense cytoplasm and prominent nucleus (Figs.205,228, 243,264,277). The young archesporium is isodiametric in shape in S. aethiopicum, S. citrullifolium, S. integrifolium, S. khasianum and S. sisymbrifolium (Figs.205,228,243,264,277). The female archesporium is generally single celled (Figs.205,228, 243,264,277). Occasionally it may be 2-celled in S. citrullifolium (Figs.229,232), 2-3 celled in S. aethiopicum and S. khasianum (Figs.206,207,265,266) and upto 4-celled in S. integrifolium and S. sisymbrifolium (Figs.244-246,278-280). In the multicellular archesporium the cells are either superposed or juxtaposed.

The female archesporium do not cut off parietal cell and directly differentiates as megaspore mother cell, which undergoes meiosis. After the first meiotic division two dyad cells are formed (Figs.209-211,233-235,247-252,267-269,281-283). The meiotic divisions in the dyad cells are generally non synchronous in S. aethiopicum and S. integrifolium (Figs.212, 213,253,254), while sometimes they may be synchronous in S. aethiopicum (Fig.214). Sometimes the division in the micropylar dyad cell may lag behind in S. aethiopicum (Figs.212,213), while in S. integrifolium the division in the chalazal dyad cell may precede that in micropylar one (Figs.253,254).

Megaspore tetrads are generally linear in S. aethiopicum, S. citrullifolium, S. integrifolium, S. khasianum and S. sisymbrifolium (Figs.215,236,256,270,284). Sometimes the megaspore tetrads may be T-shaped in S. aethiopicum, S. integrifolium and S. sisymbrifolium (Figs.216,260,285) and exceptionally inverted T-shaped in S. aethiopicum and S. citrullifolium (Figs. 217,237).

Generally the chalazal megaspore remains healthy and the three micropylar ones degenerate (Figs.218,238,257,271,286). Exceptionally the micropylar megaspore may remain healthy and remaining three degenerate in S. citrullifolium (Fig.239). Considerable variations in the number and position of healthy megaspores in a tetrad have been observed. In an exceptional case in S. khasianum the second megaspore from the chalazal side is healthy (Fig.272). In S. aethiopicum, S. integrifolium, S. khasianum and S. sisymbrifolium the two megaspores situated at the chalazal side may be healthy and rest degenerate (Figs.219, 238,273,287). Sometimes in S. integrifolium and S. sisymbrifolium the micropylar and chalazal megaspores are healthy (Figs. 259,288). Sometimes in S. aethiopicum and S. citrullifolium the chalazal and 2nd megaspore from micropylar side may remain healthy and rest two degenerate (Figs.220,240). In few cases in S. aethiopicum, S. citrullifolium and S. khasianum the two chalazal and one micropylar megaspores are healthy (Figs.222, 241,274). Rarely two micropylar and one chalazal megaspores are healthy in S. aethiopicum and S. citrullifolium (Figs.223,242).

Exceptionally in S. aethiopicum in an inverted T-shaped tetrad the micropylar megaspore degenerates and rest three remain healthy (Fig.217). In a similar case in S. citrullifolium the two chalazal and one micropylar megaspores are healthy (Fig.237). In S. integrifolium in a T-shaped tetrad one of the two micropylar and one chalazal megaspores are healthy (Fig.260), whereas in a similar case in S. sisymbrifolium both micropylar megaspores are healthy and rest two are degenerated (Fig.285). Exceptionally in S. aethiopicum two linear megaspore tetrads are situated side by side, whose two chalazal megaspores are healthy and two micropylar ones have degenerated (Fig.224).

In S. aethiopicum, S. citrullifolium, S. integrifolium and S. khasianum in a number of cases some cells of the integument enlarge considerably and behave as accessory archesporium. These cells possess dense cytoplasm and prominent nuclei. In S. citrullifolium single accessory archesporial cell is situated below the female archesporial cell (Fig.230). Rarely two accessory archesporial cells may be situated below the linear megaspore tetrad in S. aethiopicum and S. khasianum (Figs.227, 275). In S.aethiopicum and S. integrifolium 2-4 accessory archesporial cells may be situated below the megaspore mother cells (Figs.225,226,261-263). In one case in S. khasianum two healthy and two degenerated accessory archesporial cells are situated towards the chalazal side of a 2-nucleate embryo sac (Fig.276).

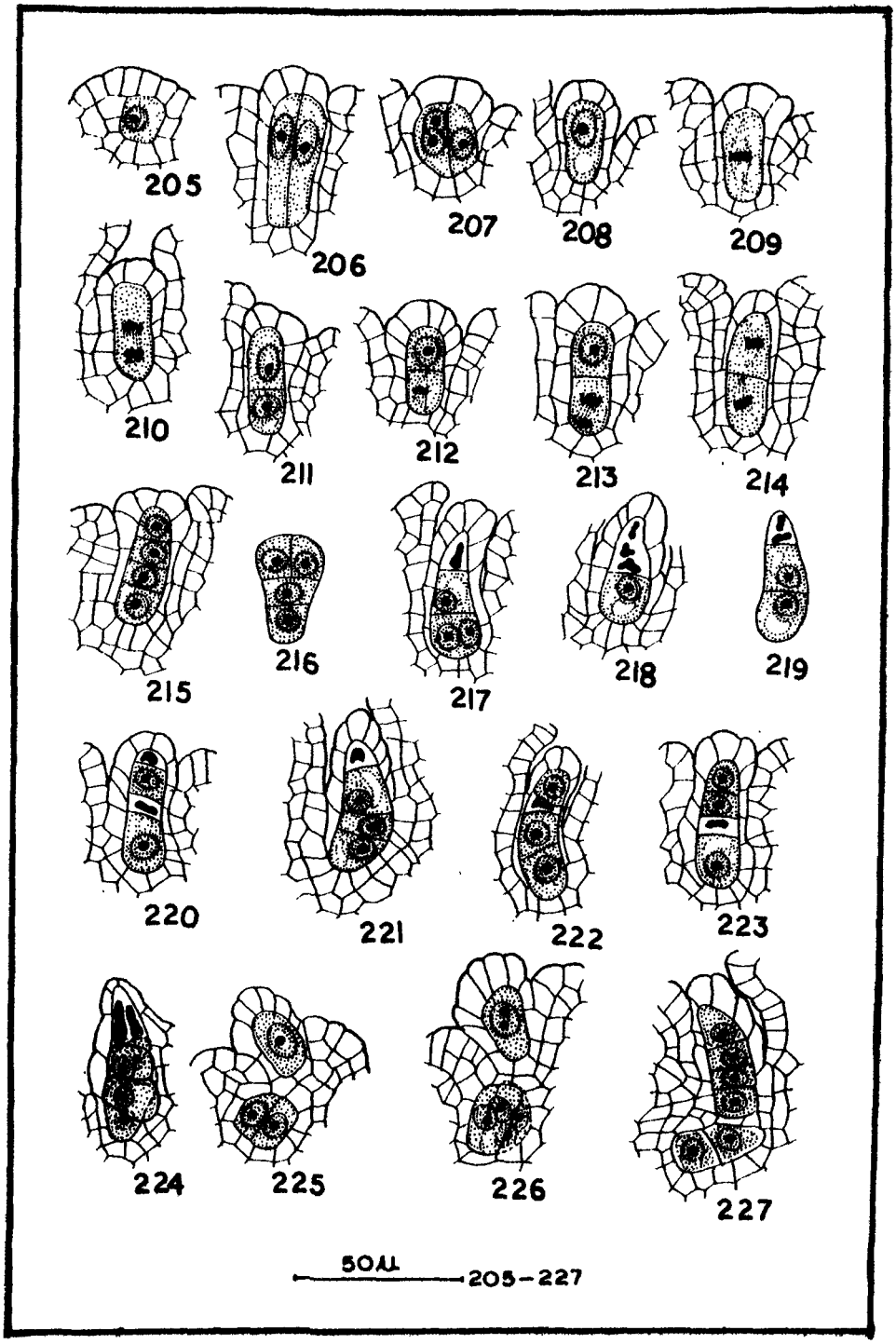
MEGASPOROGENESIS

DISTINGUISHING CHARACTERS

Characters	S. aethiopicum	S. citrullifolium	S. integrifolium	S. khasianum	S. sisymbrifolium
Female archesporium	Single celled occasionally 2-3 celled	Single celled occasionally 2-celled	Single celled occasionally upto 4-celled	Single celled occasionally 2-3 celled	Single celled occasionally upto 4-celled
Accessory archesporium	Present	Present	Present	Present	Present
Megaspore	Linear sometime T-shaped exceptionally inverted T-shaped	Linear, rarely inverted T-shaped	Linear sometime T-shaped	Linear	Linear sometime T-shaped
Functional megaspore	Chalazal	Chalazal Rarely micropylar	Chalazal	Chalazal Rarely 2nd from chalazal	Chalazal

Explanation of figures

Figs.205-227. *S. aethiopicum*. Megasporogenesis. Figs. 205-207. L.s. part ovules showing 1-3-celled female archesporium respectively. Fig.208. Megaspore mother cell. Figs.209,210. Megaspore mother cells at metaphase-I and anaphase-I respectively. Fig.211. Dyad. Figs.212, 213. The chalazal dyad cells undergoing division. Fig.214. Both the dyad cells are dividing transversely. Fig.215. Part of ovule showing linear megaspore tetrad. Fig.216. T-shaped megaspore tetrad. Fig.217. Inverted T-shaped megaspore tetrad. Fig.218. Chalazal functional megaspore. Fig.219. The two chalazal megaspores are healthy and two micropylar ones have degenerated. Fig.220. Chalazal and second megaspore from micropylar side are healthy. Fig.221. Three chalazal megaspores are healthy. Fig.222. Two chalazal and one micropylar megaspores are healthy. Fig.223. Two micropylar and one chalazal megaspores are healthy. Fig.224. Two linear megaspore tetrads situated side by side. The two chalazal megaspores in each tetrad are healthy and two micropylar ones degenerated. Figs.225, 226. Two and four accessory archesporial cells situated below the megaspore mother cells respectively. Fig.227. Two accessory archesporial cells below the linear megaspore tetrad.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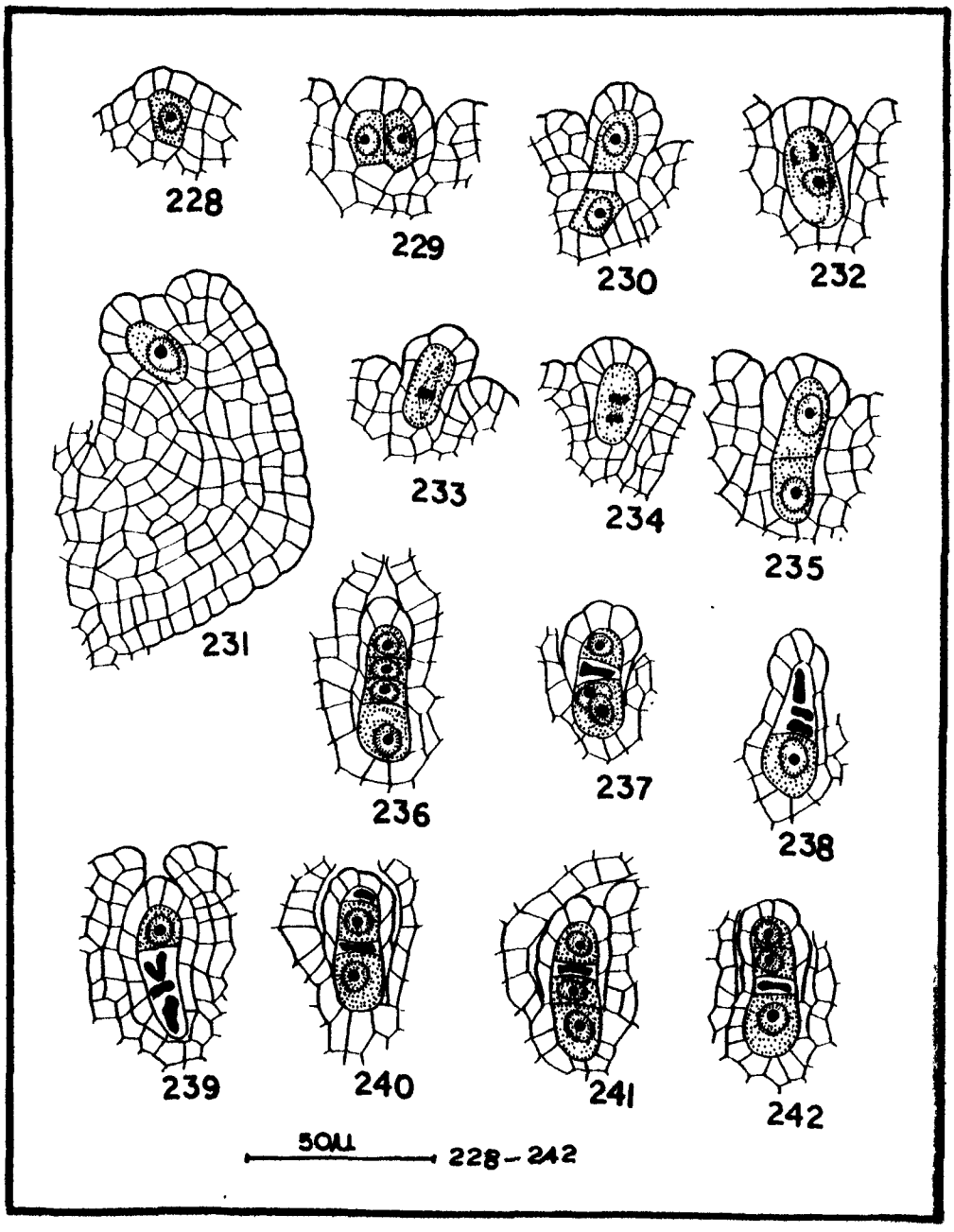
Explanation of figures

Figs.228-242. *S. citrullifolium*. Megasporogenesis. Figs. 228,229. One and two celled female archesporium respectively. Fig.230. One accessory archesporial cell below the megaspore mother cell. Fig.231. L.s. ovule showing megaspore mother cell. Fig.232. Two megaspore mother cells are situated side by side, one of them at anaphase-I stage. Figs.233,234. Megaspore mother cells at metaphase-I and anaphase-I stages respectively. Fig.235. Dyad. Fig.236. Linear megaspore tetrad. Fig.237. Inverted T-shaped megaspore tetrad. Fig.238. Chalazal functional megaspore. Fig.239. Micropylar healthy megaspore and three chalazal ones degenerated. Fig.240. Chalazal and second megaspore from micropylar side are healthy and rest two degenerated. Fig.241. Two chalazal and micropylar megaspores are healthy. Fig.242. Chalazal and two micropylar megaspores are healthy.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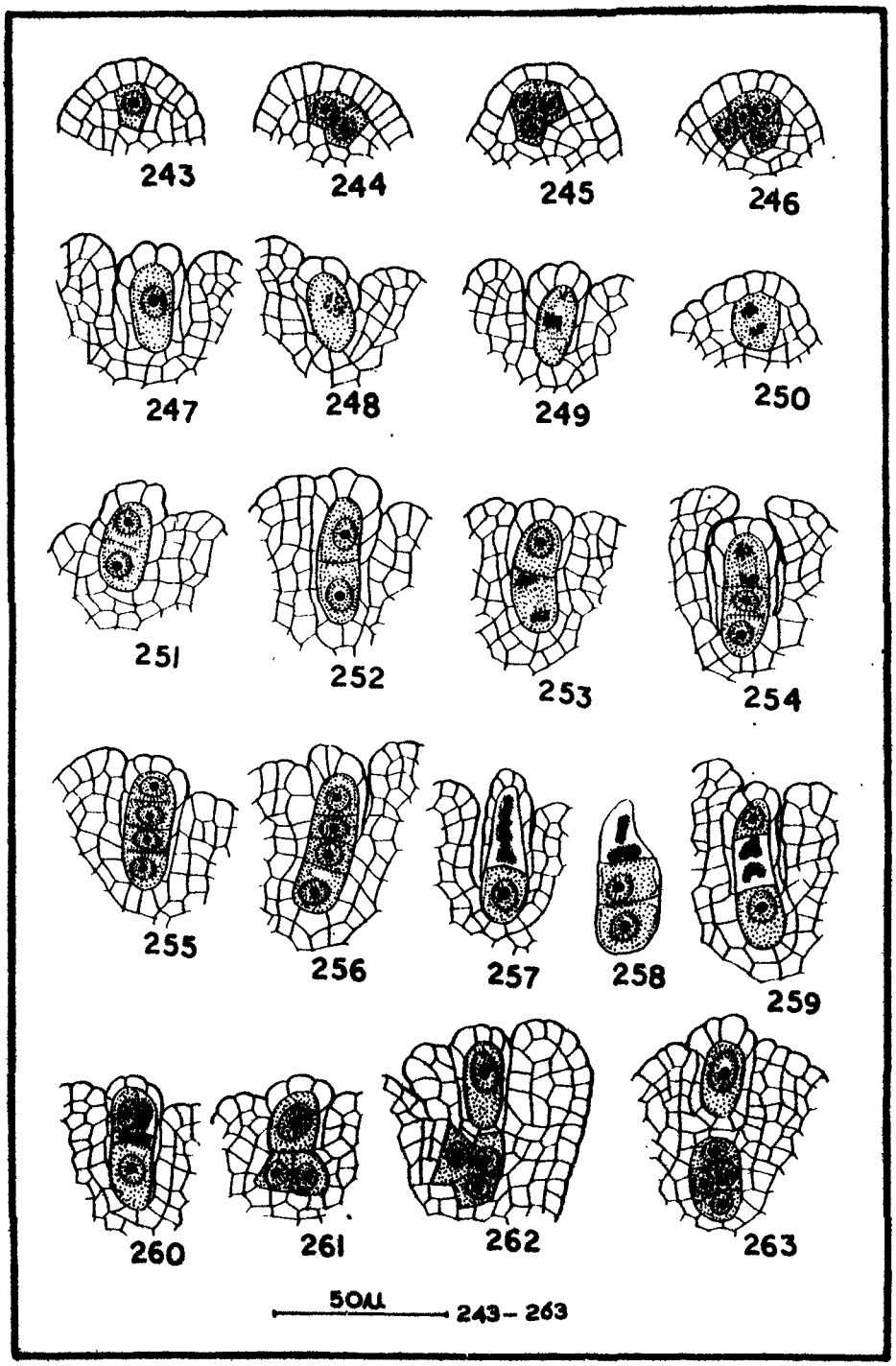
Explanation of figures

Figs.243-263. *S. integrifolium*. Megasporogenesis. Figs. 243-246. 1-4 celled female archesporium respectively. Fig.247. Megaspore mother cell. Figs.248-251. Megaspore mother cells at diakinesis, metaphase-I, anaphase-I and telophase-I respectively. Fig.252. Dyad. Fig.253. Chalazal dyad cell undergoing division. Fig.254. Micropylar dyad cell at anaphase and chalazal one at telophase stage. Fig.255. Both the dyad cells at telophase stage. Fig.256. Linear megaspore tetrad. Fig.257. Chalazal megaspore is healthy. Fig.258. Two chalazal megaspores are healthy while two micropylar ones have degenerated. Fig.259. Chalazal and micropylar megaspores are healthy while 2 middle ones degenerated. Fig.260. T-shaped megaspore tetrad. Figs.261-263. 2-4 accessory archesporial cells below the megaspore mother cells respectively.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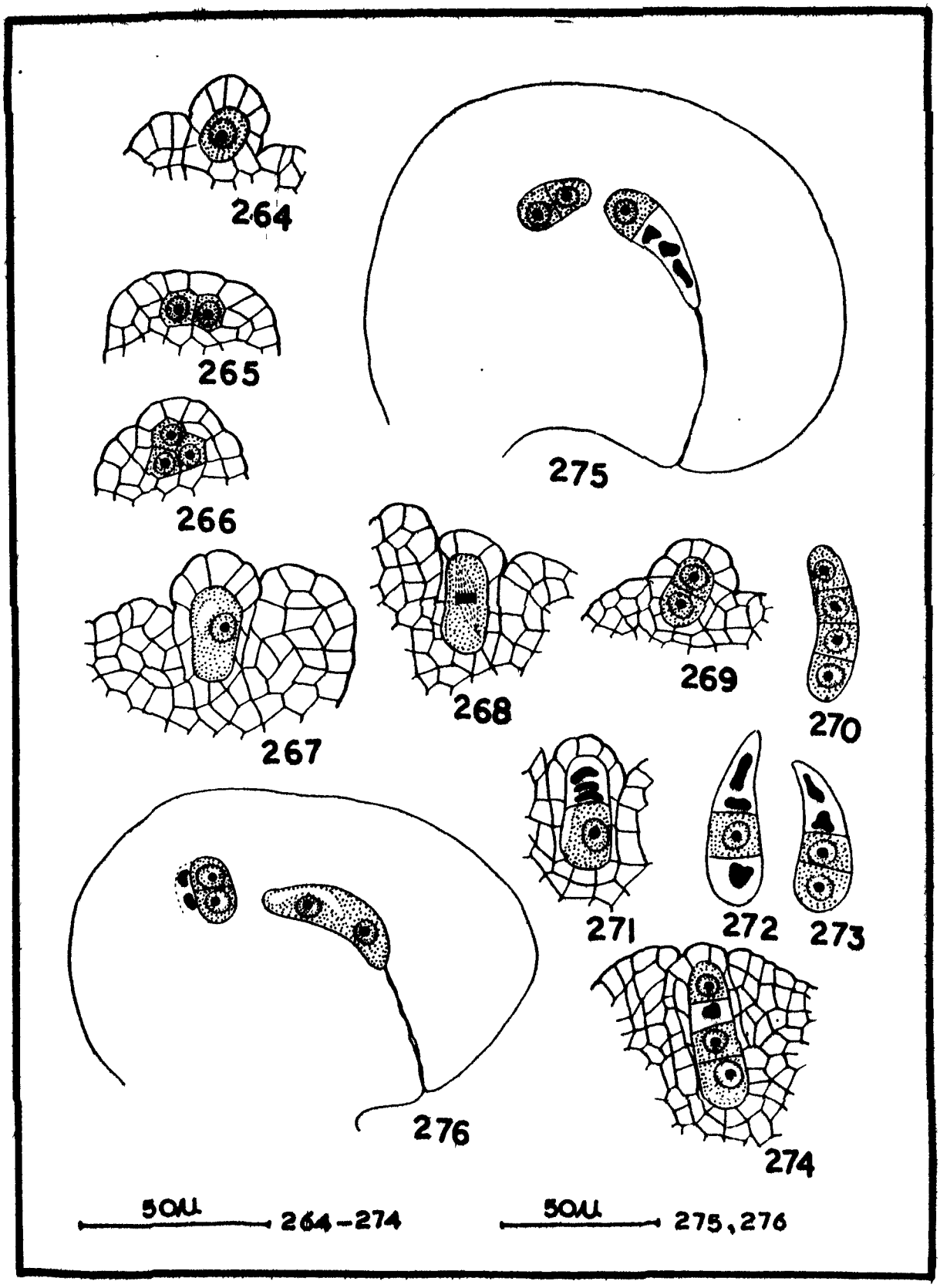
Explanation of figures

Figs.264-276. *S. khasianum*. Megasporogenesis. Figs. 264-266. 1-3-celled female archesporium respectively. Fig.267. Megaspore mother cell. Fig.268. Megaspore mother cell at metaphase-I of meiosis. Fig.269. Dyad. Fig.270. Linear megaspore tetrad. Fig.271. Chalazal megaspore is functional while the rest three have degenerated. Fig.272. Second megaspore from chalazal side is healthy while the other three have degenerated. Fig.273. Two chalazal megaspores are healthy and two micropylar ones degenerated. Fig.274. Two chalazal and one micropylar megaspores are healthy. Fig.275. Two accessory archesporial cells below the functional megaspore. Fig.276. Two healthy and two degenerated accessory archesporial cells below the 2-nucleate embryo sac.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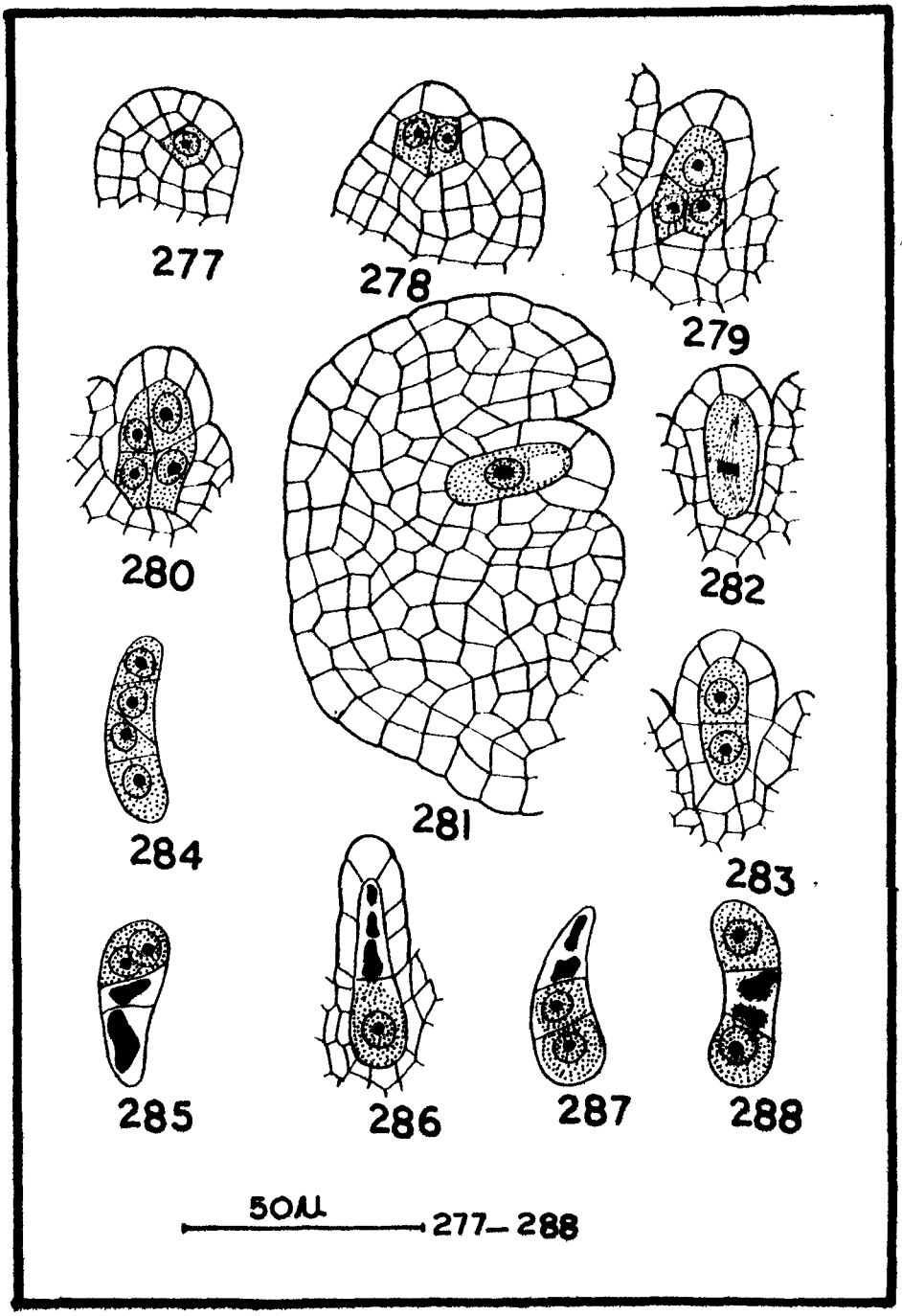
Explanation of figures

Figs.277-288. *S. sisymbrifolium*. Megasporogenesis. Figs. 277-280. 1-4-celled female archesporium respectively. Fig.281. L.s. ovule showing megaspore mother cell. Fig. 282. Megaspore mother cell at metaphase-I stage. Figs. 283,284. Dyad and linear megaspore tetrad respectively. Fig.285. T-shaped megaspore tetrad, whose both the micropylar megaspores are healthy and two chalazal ones have degenerated. Fig.286. Chalazal functional megaspore. Fig.287. Two chalazal megaspores are healthy while two micropylar ones degenerated. Fig.288. Chalazal and micropylar megaspores are healthy while two middle ones degenerated.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FEMALE GAMETOPHYTE

The development of female gametophyte in the species described here conforms to the Polygonum type. The functional megaspore enlarges considerably and its cytoplasm becomes vacuolated (Figs.289,299,309,327,343). The centrally situated nucleus divides mitotically forming two nuclei resulting into 2-nucleate embryo sac (Figs.290,300,311,328,329,344). The two nuclei remain close together for a time, but soon the embryo sac begins to enlarge and the nuclei move apart to the opposite poles of the sac. Thus a large central vacuole is formed (Figs. 291,301,312,330,345).

The division in the nuclei of the 2-nucleate embryo sac may be simultaneous in S. citrullifolium and S. integrifolium (Figs.302,313). Occasionally the division may not be synchronous in S. integrifolium (Fig.314). The two nuclei, one at each pole, divide and 4-nucleate embryo sac is formed (Figs. 292,303,315,331,346). The third nuclear division in the embryo sac is synchronous except in S. integrifolium and S. nicaymbrifolium (Figs.316,347). Ultimately 8-nucleate embryo sac is formed having four nuclei at each pole (Figs.304,317,332,333, 348).

The three nuclei of the micropylar quartet give rise to a well organized egg apparatus at the extreme apex of the sac. The egg apparatus is composed of an egg cell and two

synergids (Figs.293,305,306,319,320,334,350). The synergids are situated side by side and the egg extends below.

The three nuclei of the chalazal quartet give rise to well organized three antipodal cells at the chalazal end of the sac (Figs.293,305,306,319,320,334,350). The antipodal cells have triangular arrangement in S. aethiopicum, S. citrullifolium, S. integrifolium, S. khasianum and S. sisymbrifolium (Figs.293,305,306,319,320,322,338,350,351,353). Exceptionally the antipodals are arranged linearly in S. citrullifolium and S. khasianum (Figs.307,334). Sometimes the antipodal cells are situated side by side in S. integrifolium, S. khasianum and S. sisymbrifolium (Figs.321,335,337,352). Exceptionally in S. sisymbrifolium the two antipodal cells are attached towards the antiraphe side and one towards the funicular side of the sac at chalazal end (Fig.354).

One nucleus from each quartet moves towards the center of the embryo sac and behaves as micropylar and chalazal polar nuclei (Figs.318,349). The two polar nuclei fuse forming secondary nucleus before the entry of pollen tube into the sac (Fig.293,306,320,334,350). Variations in the number and arrangement of nuclei in female gametophyte have been observed. Rarely in S. aethiopicum in a 2-nucleate embryo sac both the nuclei are situated at the micropylar end of the sac instead of being at their respective poles (Fig.294). Similarly 5 and 8 nuclei may be aggregated towards the micropylar end of the sac in S. integ-

rifolium and S. khasianum respectively (Figs.323,339). In one case in S. aethiopicum in a 4-nucleate embryo sac two cells are organized at the micropylar end and two free nuclei are seen at the chalazal end of the sac (Fig.295). In another case in a 3-nucleate embryo sac the egg apparatus is composed of only egg and two free nuclei are seen in the center of the sac (Fig.296). Exceptionally in S. khasianum in a 7-nucleate embryo sac there is a 3-celled egg apparatus, where the egg is at the extreme apex of the sac and the two synergids are situated laterally, three free nuclei are seen at the chalazal end and one nucleus in the center of the sac (Fig.336). In S. integrifolium, S. khasianum and S. sisymbrifolium in an organized embryo sac the two synergids are situated at the apex of the sac and the egg is attached to the sac wall below the synergids (Figs.322,335, 353). In one case in S. citrullifolium it appears that the egg and one of the synergids is at the top of the sac, while the other synergid is organized below them (Fig.307). In another case the egg is situated at the top of the sac and the synergids are organized towards the free and funicular side of the sac in S. khasianum (Fig.338). Occasionally in S. sisymbrifolium the egg cell enlarges considerably and reaches upto the center of the sac (Figs.351,354). In another case in an organized embryo sac the egg apparatus is situated at the funicular side of the sac wall instead at the micropylar end and the cells are facing towards the micropyle (Fig.352).

Occurrence of twin sacs is a common feature in the species described here.

In S. aethiopicum and S. citrullifolium the two sacs having one nucleus each are placed one above the other (Figs. 297,308). In a similar case in S. sisymbrifolium the two sacs are placed side by side (Fig.355). Sometimes in S. integrifolium in a twin sac the micropylar sac is uninucleate and chalazal one 2-nucleate (Fig.324). Sometimes in S. khasianum and S. sisymbrifolium two sacs are 2-nucleate each and placed one above the other (Figs.340,356). Similarly in S. aethiopicum, S. integrifolium, S. khasianum and S. sisymbrifolium the twin sacs at 2-3 nucleate stage are placed one above the other (Figs.298,325,341,357). In a similar case in S. integrifolium the twin sacs are at 3-nucleate stage. One of the nucleus in the chalazal sac is dividing (Fig.326). In one case in S. sisymbrifolium both the sacs are at 4-nucleate stage (Fig.358). In another case the micropylar sac consists of an organized 3-celled egg apparatus and six free nuclei are seen in the chalazal sac (Fig.359). In a similar case in S. khasianum in the micropylar sac there is a 3-celled egg apparatus and two free nuclei below the egg apparatus while in the chalazal sac there are two cells at the chalazal end and one free nucleus (Fig.342). Sometimes the female gametophyte may degenerate at different stages of development in S. sisymbrifolium. In one case it appears that four accessory archesporial cells are situated at the chalazal end of the mature degenerated sac (Fig.360).

The occurrence of embryo sac with less than eight nuclei may be interpreted due to suppression of second or third mitotic division in the nuclei of either pole .

The occurrence of twin sacs in the species described here may be interpreted that they might develop from the two functional megaspores of the same megaspore tetrad or from twin megaspore tetrad.

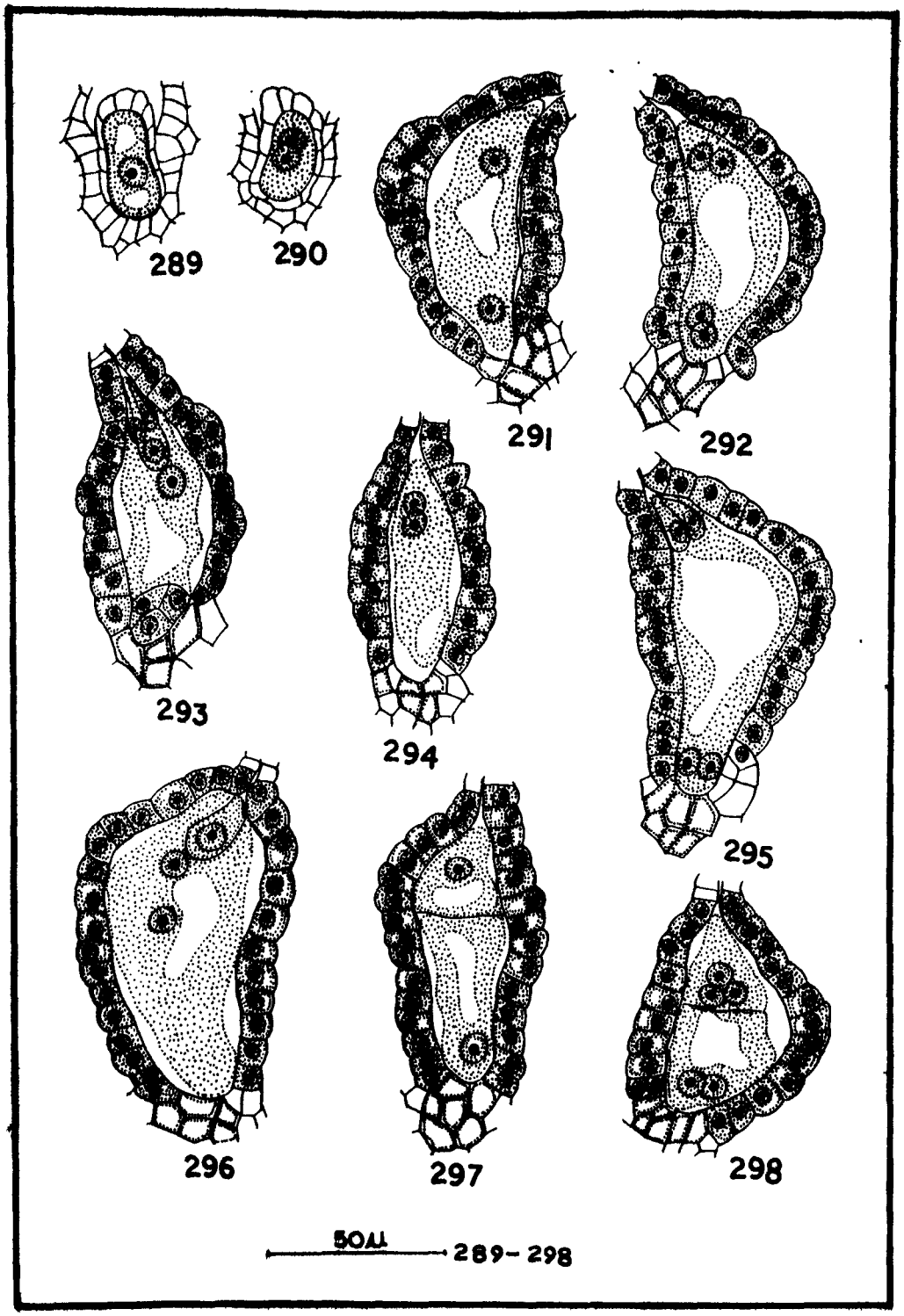
FEMALE GAMETOPHYTE

DISTINGUISHING CHARACTERS

Characters	*S. subhimalense*	*S. citrullifolium*	*S. integrifolium*	*S. khasianum*	*S. pinnatifolium*
Female gametophyte	Monosporic 8-nucleat polygonum type	Monosporic 8-nucleate Polygonum type	Monosporic 8-nucleate Polygonum type	Monosporic 8-nucleate Polygonum type	Monosporic 8-nucleate Polygonum type
Fusion of polar nuclei	Secondary nucleus	Secondary nucleus	Secondary nucleus	Secondary nucleus	Secondary nucleus
Twin sacs	Present	Present	Present	Present	Present

Explanation of figures

Figs.289-298. *S. aethiopicum*. Female gametophyte. Fig. 289. Functional megaspore with terminal vacuoles. Figs. 290,291. 2-nucleate embryo sacs. Fig.292. 4-nucleate embryo sac. Fig.293. Mature embryo sac with 3-celled egg apparatus, 3 antipodal cells and a secondary nucleus. Fig.294. 2-nucleate embryo sac; both the nuclei are situated at the micropylar end. Fig.295. 4-nucleate embryo sac showing two free nuclei at chalazal end and two cells towards the micropylar end. Fig.296. 3-nucleate embryo sac showing an egg cell and two free nuclei. Fig.297. Two uninucleate embryo sacs situated one above the other. Fig. 298. Twin embryo sacs; the micropylar sac is 3-nucleate while the chalazal one 2-nucleate.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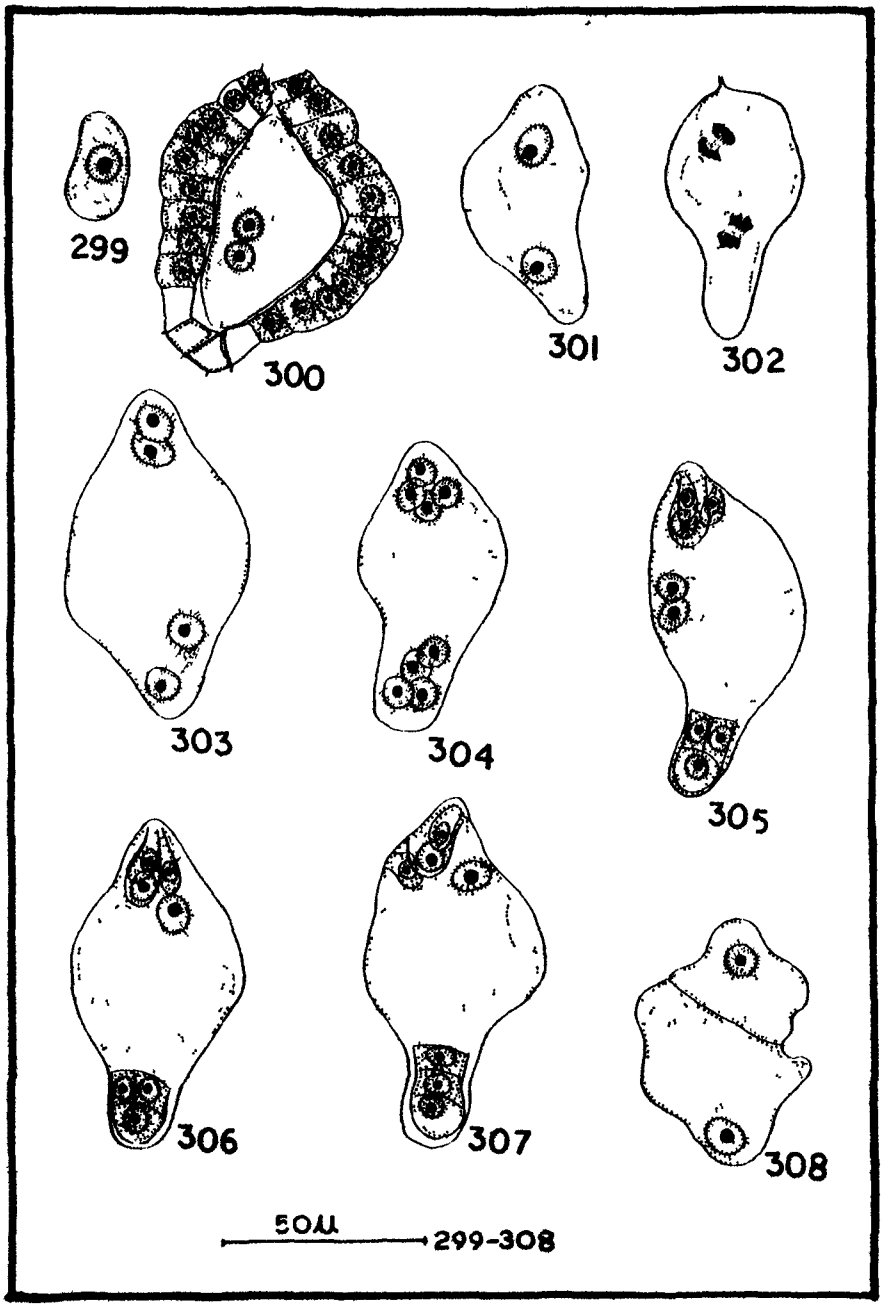
Explanation of figures

Figs.299-308. *S. citrullifolium*. Female gametophyte. Fig.299. Functional megaspore. Figs.300, 301. 2-nucleate embryo sacs. Fig.302. Both the nuclei of 2-nucleate embryo sac are dividing. Figs.303, 304. 4 and 8-nucleate embryo sacs respectively. Fig.305. Mature embryo sac having 3-celled egg apparatus, three antipodal cells and two polar nuclei. Fig.306. Mature embryo sac, polar nuclei have fused to form secondary nucleus. Fig.307. Mature embryo sac showing linear arrangement of antipodal cells. Fig.308. Twin embryo sacs.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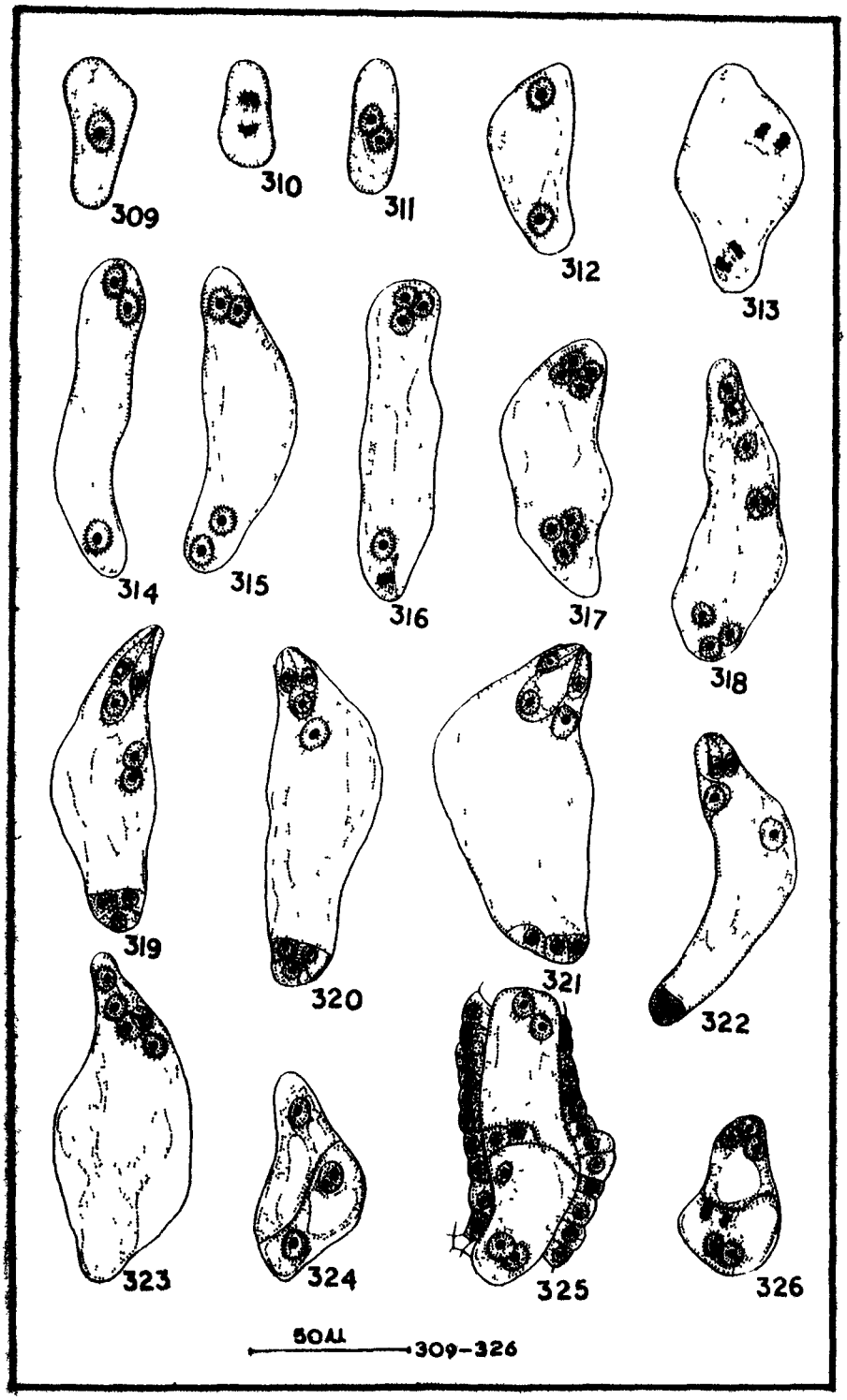
Explanation of figures

Figs.309-326. *S. integrifolium*. Female gametophyte. Fig. 309. Functional megaspore. Fig.310. Dividing functional megaspore. Figs.311, 312. 2-nucleate embryo sacs. Fig. 313. The nuclei of 2-nucleate embryo sac are dividing. Figs.314,315. Three and four nucleate embryo sacs respectively. Fig.316. Five nucleate embryo sac; one of the two nuclei of chalazal end is dividing. Fig.317. 8-nucleate unorganized embryo sac. Fig.318. 8-nucleate embryo sac, one nucleus from each quartet has moved to the centre. Fig. 319. Mature embryo sac having 3-celled egg apparatus, three antipodal cells and two polar nuclei. Fig.320. Mature embryo sac; the two polar nuclei have fused. Fig.321. Mature embryo sac; the antipodal cells are arranged side by side. Fig.322. Mature embryo sac, the synergids are situated at the micropylar side while the egg below them. Fig.323. 5-nucleate embryo sac, the nuclei are aggregated at the micropylar end. Figs.324-326. Twin embryo sacs.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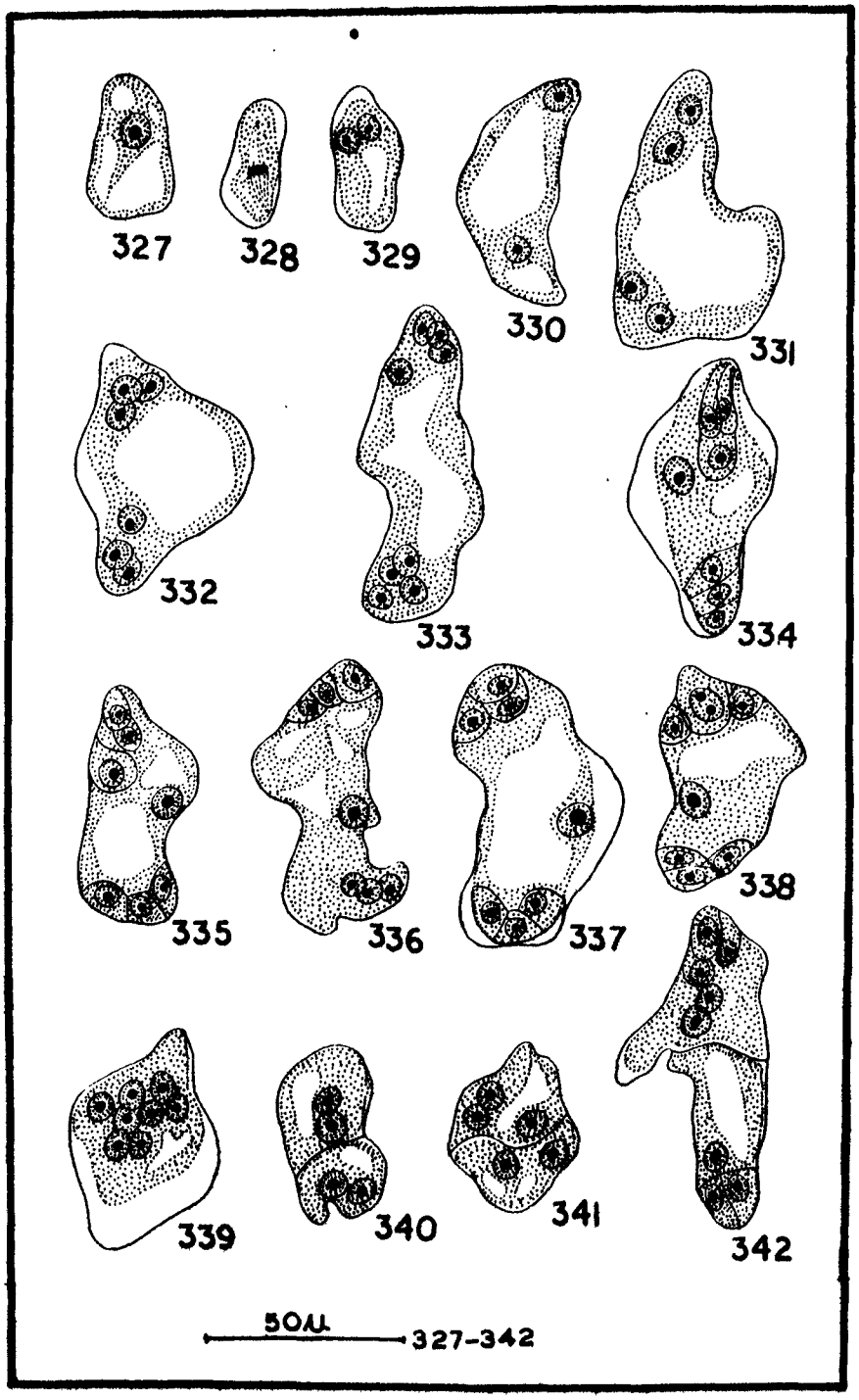
Explanation of figures

Figs.327-342. *S. khasianum*. Female gametophyte. Fig.327. Functional megaspore. Fig.328. Dividing functional megaspore. Figs.329,330. 2-nucleate embryo sacs. Figs.331-333. Four, six and 8-nucleate embryo sacs respectively. Fig.334. Mature embryo sac having 3-celled egg apparatus, three linearly arranged antipodal cells and secondary nucleus. Fig.335. Mature embryo sac, the antipodal cells are arranged side by side, the two synergids are situated at the micropylar end and the egg below them. Fig.336. 7-nucleate embryo sac, the cells of the egg apparatus are placed side by side at the micropylar end, there are three free nuclei at the chalazal end/and one in the centre. Fig.337. Mature embryo sac; the antipodal cells are arranged side by side and the cells of egg apparatus are of equal size. Fig.338. Mature embryo sac, the cells of egg apparatus are situated side by side at the apex of the sac. Fig.339. 8-nucleate embryo sac; all the nuclei are aggregated. Figs.340-342. Twin embryo sacs.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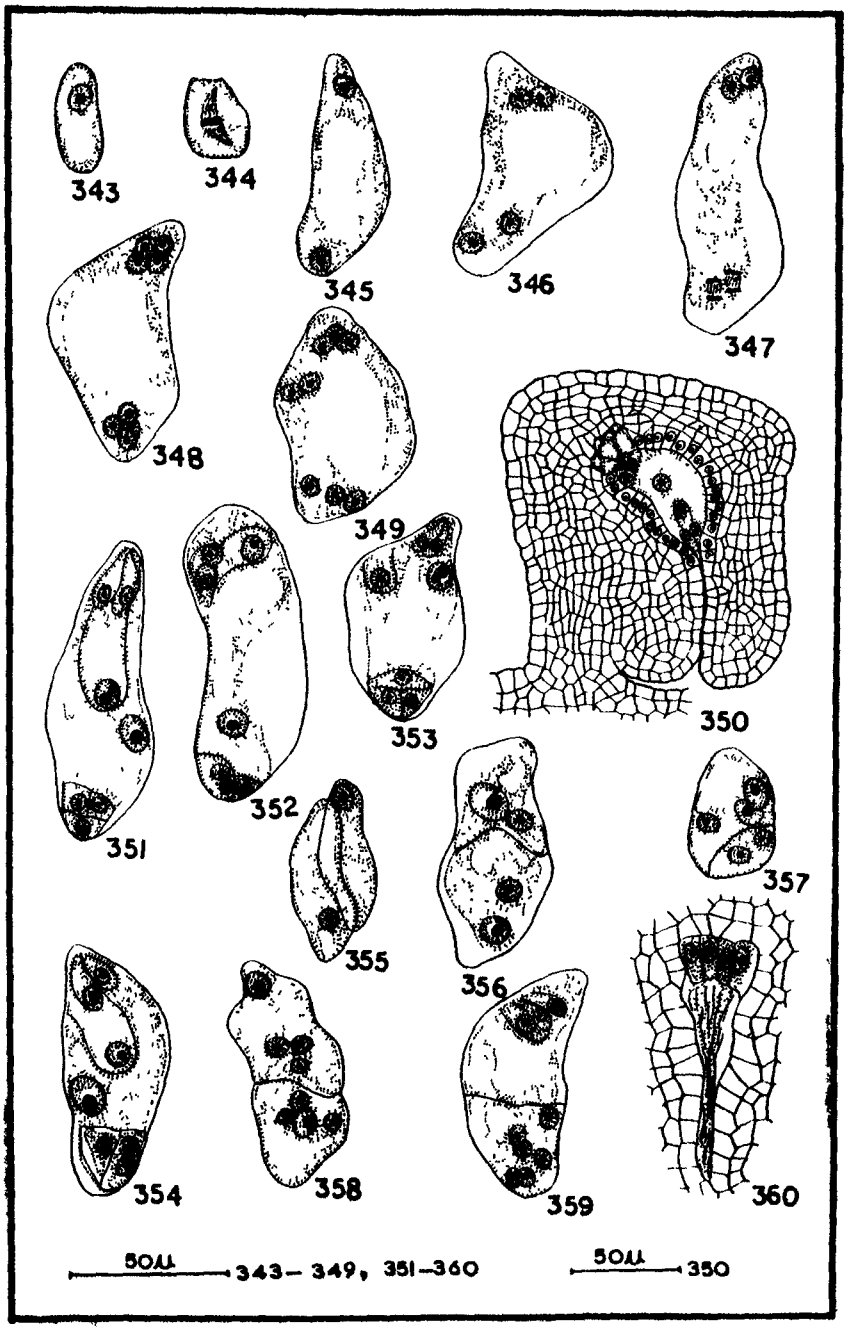
Explanation of figures

Figs.343-360. *S. nicrobrifolium*. Female gametophyte. Fig. 343. Functional megaspore. Fig.344. Dividing functional megaspore. Figs.345, 346. 2 and 4-nucleate embryo sacs respectively. Fig.347. 4-nucleate embryo sac, the two nuclei at the chalazal end are dividing. Figs.348,349. 8-nucleate unorganised embryo sacs. Fig.350. L.s. ovule showing mature embryo sac. Fig.351. Mature embryo sac, the egg cell extends upto the centre of the sac. Fig.352. Mature embryo sac, the egg apparatus is situated on the funicular side. Fig.353. Mature embryo sac; note the position of the egg. Fig.354. Mature embryo sac; note the arrangement of antipodals. Fig. 355. Uninucleate embryo sacs situated side by side. Figs. 356-358. Twin embryo sacs placed one above the other. Fig. 359. Twin sacs; the 3-nuclei of the micropylar sac have organised into egg apparatus while the chalazal sac is 6-nucleate. Fig.360. Four accessory archesporial cells situated at the chalazal end of degenerated sac.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POLLINATION AND COURSE OF POLLEN TUBE

The stigma is bilobed and papillate in *S. aethiopicum*, *S. citrullifolium*, *S. integrifolium*, *S. khasianum* and *S. sisymbrifolium* (Figs.361-363,366-368), occasionally three lobedin *S. integrifolium* (Fig.364). It remains straight through out in *S. aethiopicum*, *S. integrifolium* and *S. khasianum* (Figs.361,363, 364,366), whereas in *S. citrullifolium* and *S. sisymbrifolium* it becomes curved immediately after pollination (Figs.362,367,368). The stigmatic papillae are with tubular tips (Fig.369). In *S. aethiopicum* and *S. citrullifolium* the two stigmatic lobes are separate upto a considerable length (Figs.361,362), while the stigma is deeply lobed in *S. integrifolium* and *S. sisymbrifolium* (Figs.363,368). In one exceptional case in *S. integrifolium* it appears that in a flower two styles developed, one of which developed fully while the other was rudimentary (Fig.365).

Pollination is anemophilleus. The pollen grains are seen entangled between the stigmatic papillae where they germinate (Fig.369). The style is solid and devoid of any special transmitting tissue for the growth of pollen tube (Figs.361-368). The pollen tubes creep between the stigmatic papillae and enter the stylar tissue. The pollen tubes grow down the stylar tissue through the intercellular spaces without damaging them, reach the base of style and enter the ovarian cacity. Thus a bundle of pollen tubes reaches the top of placenta. Later, the pollen tubes move in all the directions on the placenta surface and enter the ovule through micropyle.

POLLINATION

DISTINGUISHING CHARACTERS

Characters	S. asthianicum	S. citrullifolium	S. integrifolium	S. khasianum	S. pierrebrifolium
Stigma	Bilobed	Bilobed	Three lobed	Bilobed	Bilobed
Stigmatic papillae	Tubular	Tubular	Tubular	Tubular	Tubular
Style	Hollow upto a considerable length	Hollow upto a considerable length	Solid, rarely hollow upto a considerable length	Solid	Solid
Pollination	Anemophileous	Anemophileous	Anemophileous	Anemophileous	Anemophileous

FERTILIZATION

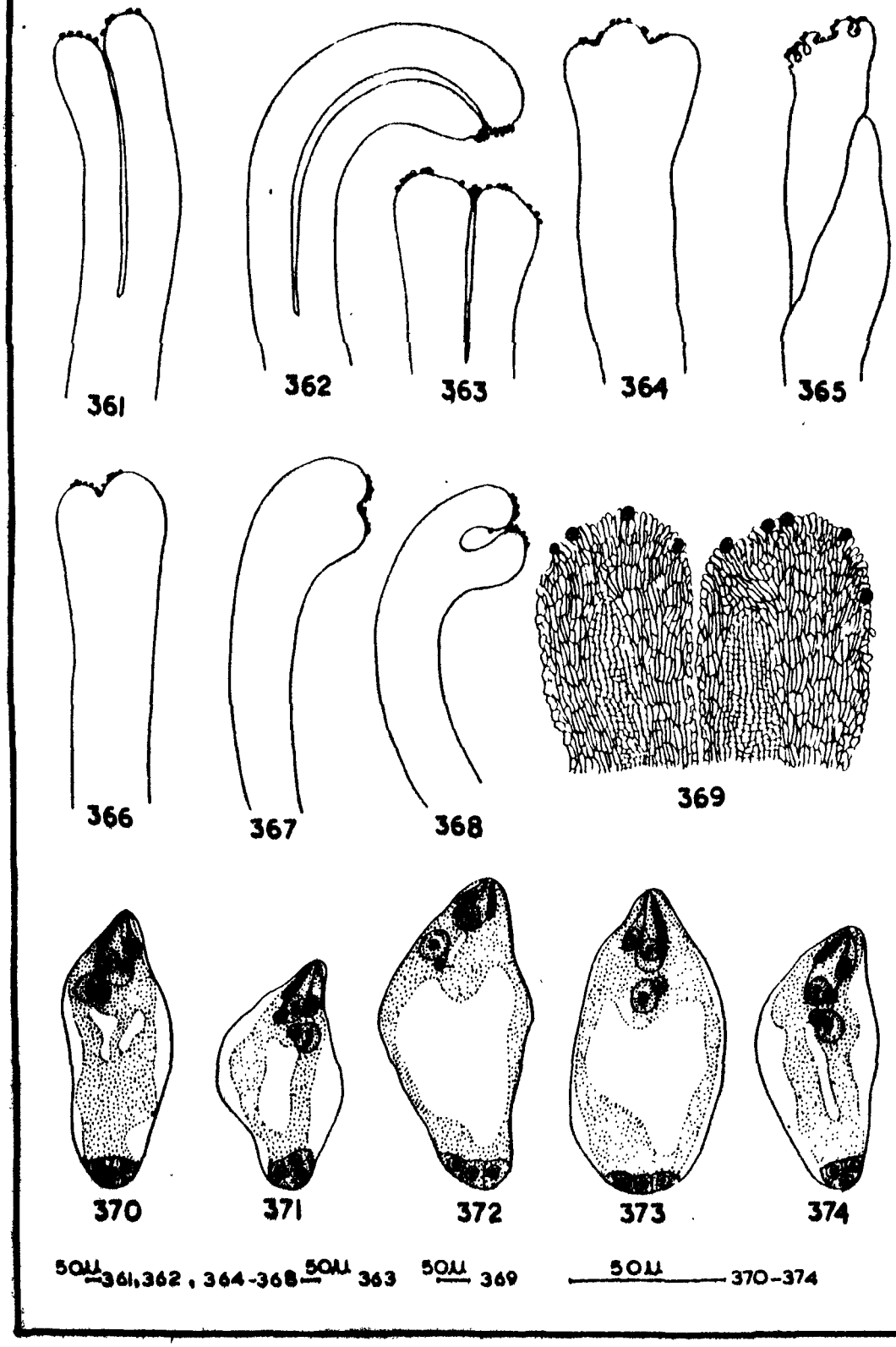
Fertilization is porogamous. The ovules situated at the top of the placenta are mature and ready to receive the pollen tube. Prior to its entry into the embryo sac the pollen tube is a delicate cylindrical structure. It becomes irregular in shape and quite conspicuous inside the sac. The pollen tube enters the sac near one of the synergids. May be, some chemotactic substance is secreted by the cells of egg apparatus or the wall of the sac is weak in that region. During the entry of the pollen tube into the embryo sac one synergid is gnerally destroyed. Later, the other synergid also degenerates.

The pollen tube burst into the embryo sac and two male gametes are released. One male gamete fuses with the egg forming zygote. The second male gamete fuses with the secondary nucleus producing a primary endosperm nucleus (Figs.370-374). The antipodals are ephemeral and usually degenerate after fertilization.

Explanation of figures

Figs.361-369. Pollination. Figs.361,369. *S. aethiopicum*. Fig.362. *S. citrullifolium*. Figs.363-365. *S. integrifolium*. Fig.366. *S. khasianum*. Figs.367,368. *S. sisymbrifolium*. Figs.370-374. *S. aethiopicum*, *S. citrullifolium*, *S. integrifolium*, *S. khasianum* and *S. sisymbrifolium* respectively. Fertilization. Figs.361-363, 366-368. L.s. bifid stigma showing pollination. Fig.364. L.s. three lobed stigma showing pollination. Fig.365. L.s. rudimentary and fully developed style with stigma. Fig.369. L.s. bifid stigma (magnified) showing stigmatic papillae and entangled pollen grains.

Figs.370-374. Embryo sacs showing stages of fertilization.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ENDOSPERM

The development of endosperm in *S. aethiopicum*, *S. citrullifolium*, *S. integrifolium*, *S. khasianum* and *S. sisymbrifolium* is *ab initio* Cellular. The development of endosperm starts immediately after fertilization, while the division of zygote is delayed unless sufficient amount of endosperm is formed. The plane of divisions in the early stages of endosperm development varies in different species described here. Thus for the sake of clarity the development of endosperm in different species has been described separately.

S. aethiopicum and *S. citrullifolium*

The development of endosperm in *S. aethiopicum* and *S. citrullifolium* is *ab initio* Cellular. The first division in the primary endosperm cell is transverse dividing the sac into a primary micropylar and primary chalazal endosperm chambers (Figs.375,376,388,389). The division in either chamber may precede the other (Figs.377-379,390,391). The division in both the primary endosperm chambers is longitudinal, thus 4-celled endosperm is formed (Figs.380,392). The division in the two juxtaposed cells of the chalazal chamber is longitudinal (Figs. 381,382,393). The two juxtaposed cells of the micropylar chamber divide transversely in *S. aethiopicum* (Figs.382,383), whereas in *S. citrullifolium* a definite sequence is not

observed. Later, the divisions become irregular forming multicellular endosperm (Figs.384,396). Sometimes in S. aethiopicum and S. citrullifolium the division in the primary chalazal endosperm chamber is transverse and longitudinal in primary micropylar endosperm chamber producing four cells arranged in T-shaped manner (Figs.385,386,394). In an exceptional case in S. citrullifolium it appears that the first division in the primary endosperm cell has been longitudinal forming 2-cells, which divide transversely (Fig.395). The cells of endosperm on maturity possess dense cytoplasm replete with starch grains (Figs.387,397). Cellulosic thickenings are deposited on the walls of mature endosperm cells in S. aethiopicum (Fig.387).

S. integrifolium

The development of endosperm is ab initio Cellular. The first division in the primary endosperm cell is transverse producing primary micropylar and primary chalazal endosperm chambers (Figs.398,399). The division in the primary chalazal endosperm chamber may precede that in micropylar chamber (Fig. 400). The division in the primary chalazal endosperm chamber is transverse and longitudinal in the primary micropylar endosperm chamber forming four cells arranged in T-shaped manner (Figs.400,401). The division in both the cells of micropylar chamber is longitudinal (Figs.403). The upper derivative of the chalazal chamber also divides in a similar plane (Figs.402,402).

Thus 7-celled endosperm is produced (Fig.403). Sometimes the division in both the primary endosperm chambers is longitudinal (Figs.404,405). Later, the two juxtaposed cells in each chamber appear to divide transversely (Fig.406). Exceptionally in one case in a 4-celled endosperm it appears that primary micropylar endosperm chamber has divided transversely and chalazal one longitudinally, thus the four cells are arranged in an inverted T-shaped manner (Fig.407). Later, the divisions become irregular forming multicellular endosperm (Fig.408). The cells of endosperm in the early stages of development possess vacuolated cytoplasm while at maturity the cytoplasm becomes replete with starch grains (Fig.409).

S. khasianum

The development of endosperm is ab initio Cellular. The first division in the primary endosperm cell is transverse producing a primary micropylar and a primary chalazal endosperm chambers (Figs.410,411). The division in the primary chalazal endosperm chamber may precede that in micropylar one (Fig.412). The division in both the endosperm chambers is longitudinal. Thus four celled endosperm is produced (Fig.413). The division in one of the two juxtaposed cells of the chalazal chamber is transverse while the division in the cells of the micropylar endosperm chamber is longitudinal forming 7-celled endosperm (Figs.414-416). Later, the divisions become irregular and multicellular endosperm is formed (Fig.425). Variations in the

plane and sequence of cell divisions occur during the early stages of endosperm development. Occasionally the primary micropylar endosperm chamber divides transversely while the chalazal chamber longitudinally. Thus four cells are arranged in an inverted T-shaped manner (Figs.417,418). Later, one of the two juxtaposed cells of chalazal chamber divides transversely and the lower cell of the micropylar chamber divides longitudinally forming 7-celled endosperm (Figs.419,420). Sometimes the primary micropylar endosperm chamber divides longitudinally and chalazal one transversely producing four cells arranged in a T-shaped manner (Fig.421). Later, both the superposed cells of the chalazal chamber divide longitudinally forming 6-celled endosperm (Figs.422,423). In one case in an eight celled endosperm it appears that the cells of both the primary endosperm chambers have divided longitudinally (Fig. 424). The cells of the endosperm possess dense cytoplasm replete with starch grains. Cellulosic thickenings are deposited on the walls of the endosperm cells, thus they appear thick walled (Fig.426).

S. nasymbrifolium

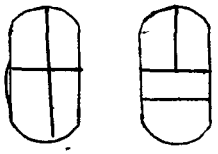
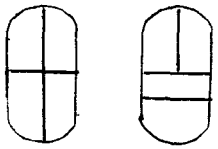
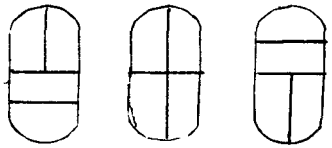
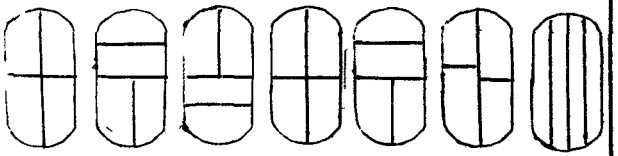
The development of endosperm is ab initio Cellular. The primary endosperm cell divides transversely forming a primary micropylar and a primary chalazal endosperm chamber (Figs.427,428). The division in either chamber may precede the other (Figs.429,430). The division in both the chambers is

longitudinal forming 4-celled endosperm (Fig.431). Later, both the juxtaposed cells of micropylar chamber divide longitudinally while those of chalazal chamber divide transversely forming 8-celled endosperm (Fig.432). Further the divisions become irregular and multicellular endosperm is formed (Fig.442).

Variations in the plane and sequence of cell divisions occur during the early stages of endosperm development. In one case it appears that the primary micropylar endosperm chamber has divided transversely and chalazal one longitudinally, thus four cells are arranged in an inverted T-shaped manner (Fig.433). In another case it appears that in a 4-celled endosperm both the juxtaposed cells of the chalazal chamber have divided longitudinally (Fig.434). In another case it seems that the cells of micropylar chamber divide transversely instead of longitudinally (Fig.435). Still in another case in a 4-celled endosperm the primary micropylar endosperm chamber has divided transversely, the lower cell of which has divided longitudinally (Fig.436). In a similar case it appears that the micropylar and chalazal cells of a 3-celled endosperm have divided vertically (Fig.437). Occasionally the division in the primary endosperm cell is vertical (Fig.438-441). Later, the division in both the cells are transverse (Figs.439,440). Exceptionally the first two divisions in the primary endosperm cells are longitudinal. Thus four cylindrical cells are formed (Fig.441). The endosperm cells at the mature stage possess dense cytoplasm replete with starch grains (Fig.443).

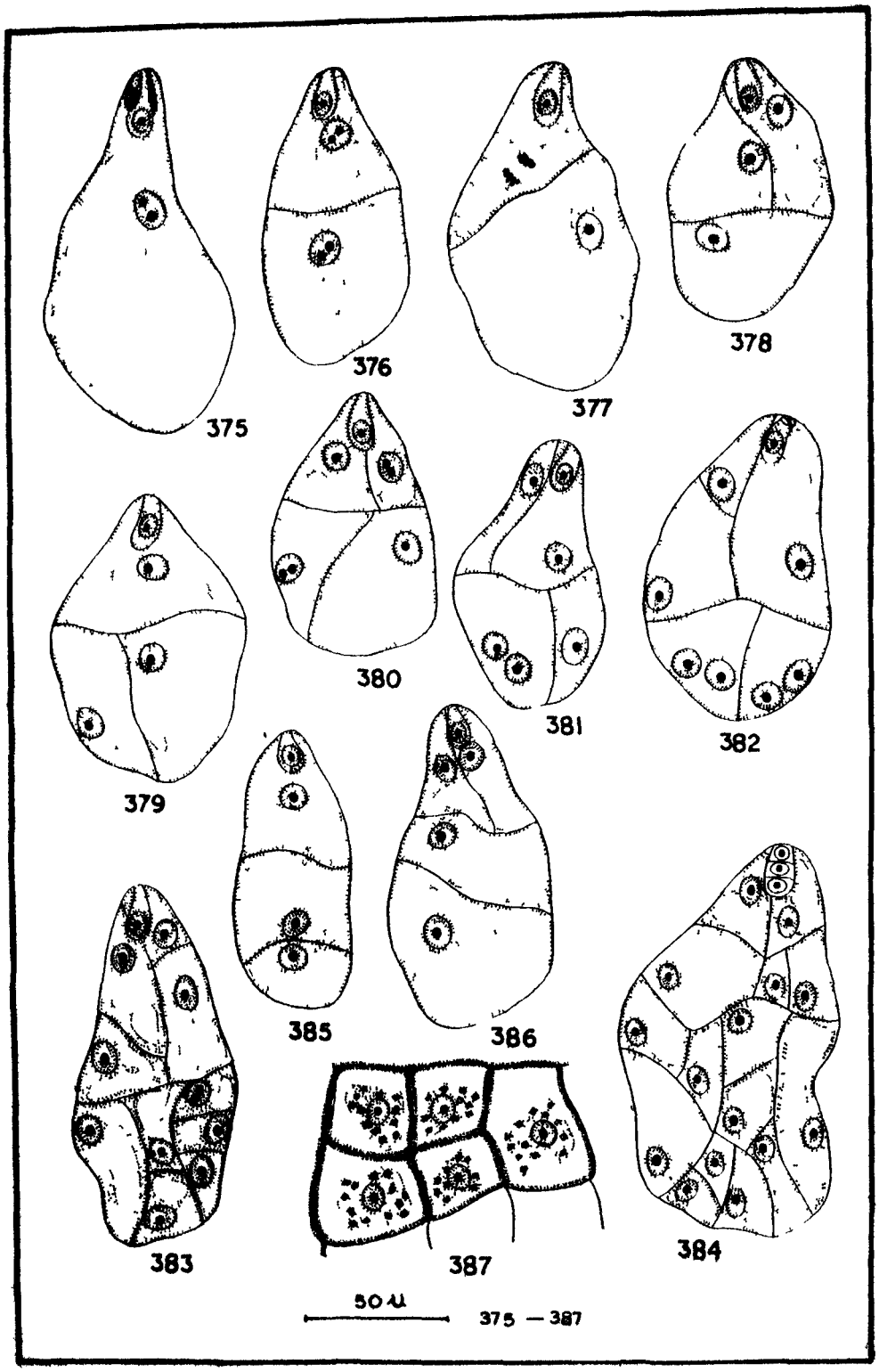
ENDOSPERM

DISTINGUISHING CHARACTERS

Characters	*S. asthiopicum*	*S. citrullifolium*	*S. integrifolium*	*S. khasianum*	*S. nigrum*
Endosperm	Cellular	Cellular	Cellular	Cellular	Cellular
First division	Transverse	Transverse, rarely longitudinal	Transverse	Transverse	Transverse, occasionally longitudinal
Second division	Longitudinal in both the primary endosperm chambers, occasionally transverse in primary chalazal chamber.	Longitudinal in both the primary endosperm chambers, rarely transverse in chalazal chamber.	Longitudinal in primary micropylar and transverse in primary chalazal endosperm chambers, occasionally longitudinal in both the primary endosperm chambers, rarely transverse in primary micropylar chamber.	Longitudinal in both the chambers, rarely transverse in either chambers.	Longitudinal in both the chambers, occasionally transverse in micropylar chamber. Ist division when longitudinal, both the chambers may divide transversely or longitudinally.
					
Mature endosperm cells	Replete with starch grains.	Replete with starch grains.	Replete with starch grains.	Replete with starch grains.	Replete with starch grains.

Explanation of figures

Figs.375–387. *S. aethiopicum*. Development of endosperm. Fig.375. Fertilized embryo sac showing zygote and primary endosperm nucleus. Figs.376,377. 2-celled endosperm. Figs. 378,379. 3-celled endosperm. Figs.380–382. Four, five and seven celled endosperm respectively. Figs.383,384. Multicellular endosperm. Fig.385. 3-celled endosperm, the chalazal endosperm chamber has divided transversely. Fig. 386. 4-celled endosperm, the cells are arranged in T-shaped manner. Fig.387. Cells of mature endosperm showing starch grains and cellulosic thickening on the walls.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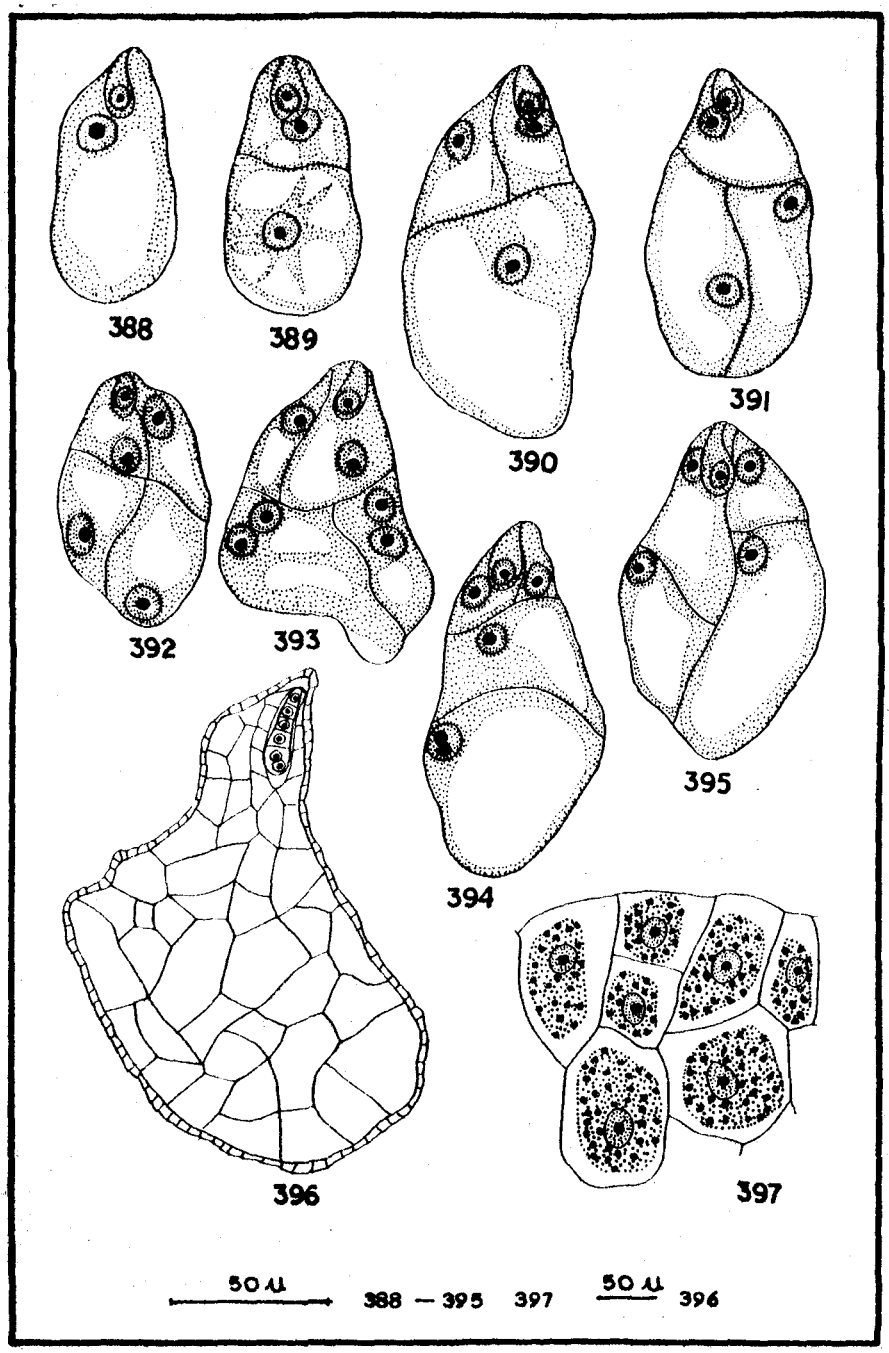
Explanation of figures

Figs.388–397. *S. citrullifolium*. Development of endosperm. Fig.388. Fertilized embryo sac showing zygote and primary endosperm nucleus. Fig.389. Two celled endosperm. Figs. 390,391. 3–celled endosperm. Fig.392. 4–celled endosperm. Fig.393. 6–celled endosperm, both the juxtaposed cells of chalazal chamber have divided longitudinally. Fig.394. 4–celled endosperm showing T–shaped arrangement. Fig.395. 4–celled endosperm, the first division in the primary endosperm cell has been longitudinal and both the resultant cells have divided transversely. Fig.396. Multicellular endosperm. Fig.397. Mature endosperm cells with dense cytoplasm replete with starch grains.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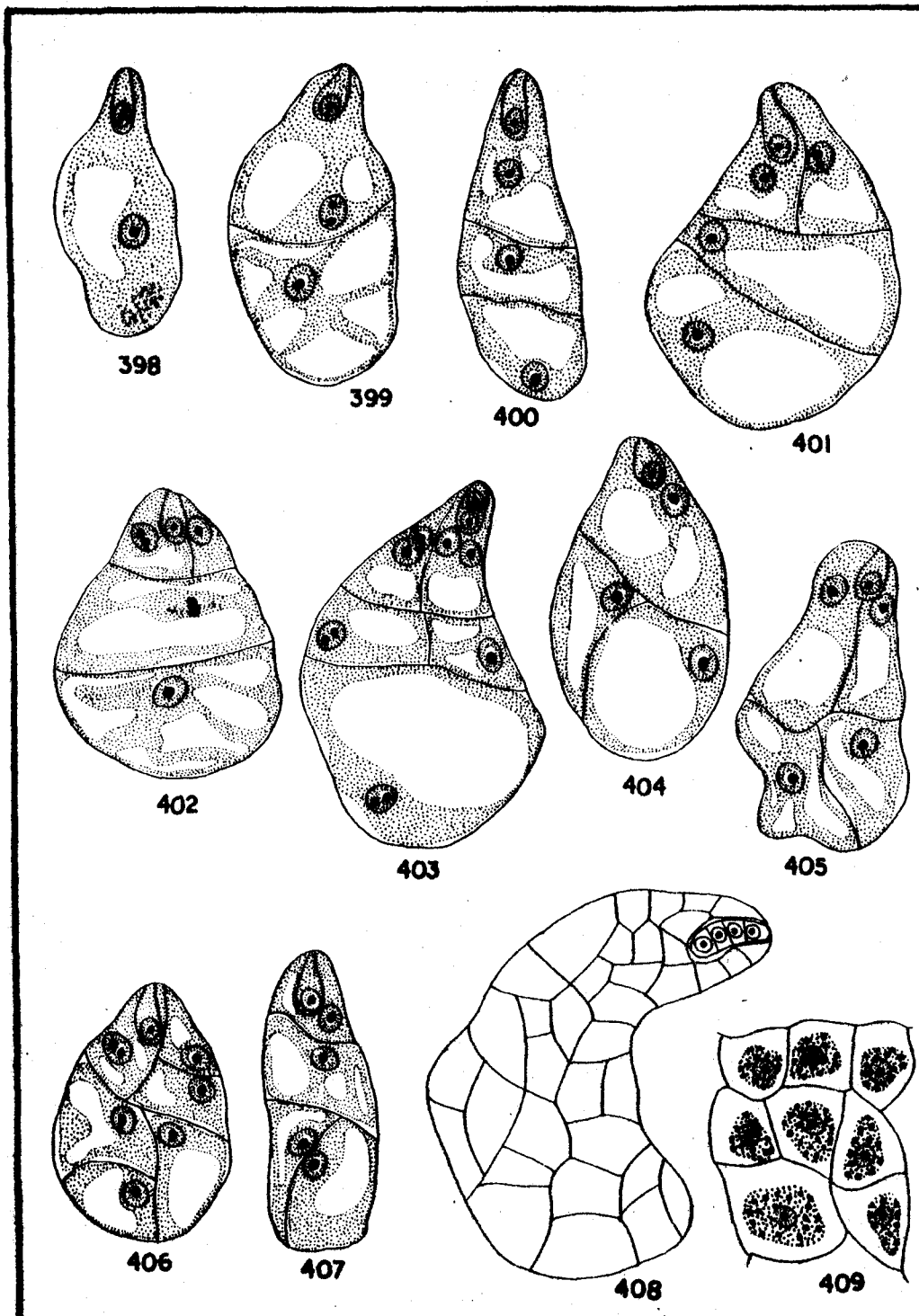
Explanation of figures

Figs.398–409. *S. integrifolium*. Development of endosperm. Fig.398. Fertilized embryo sac showing zygote and primary endosperm nucleus. Fig.399. 2-celled endosperm. Fig.400. 3-celled endosperm, the primary chalazal endosperm chamber has divided transversely. Fig.401. 4-celled endosperm showing T-shaped arrangement. Fig.402. 4-celled endosperm, the second cell from the chalazal side is dividing. Fig.403. 7-celled endosperm with 2-celled proembryo, both the cells of micropylar chamber have divided vertically. Fig.404. 3-celled endosperm, primary chalazal endosperm chamber has divided vertically. Fig.405. 4-celled endosperm. Fig.406. 6-celled endosperm, one of the two juxtaposed cells of each chamber has divided transversely. Fig.407. 4-celled endosperm showing inverted T-shaped arrangement. Fig.408. Multicellular endosperm at linear proembryonic tetrad stage. Fig.409. Cells of mature endosperm showing dense cytoplasm replete with starch grains.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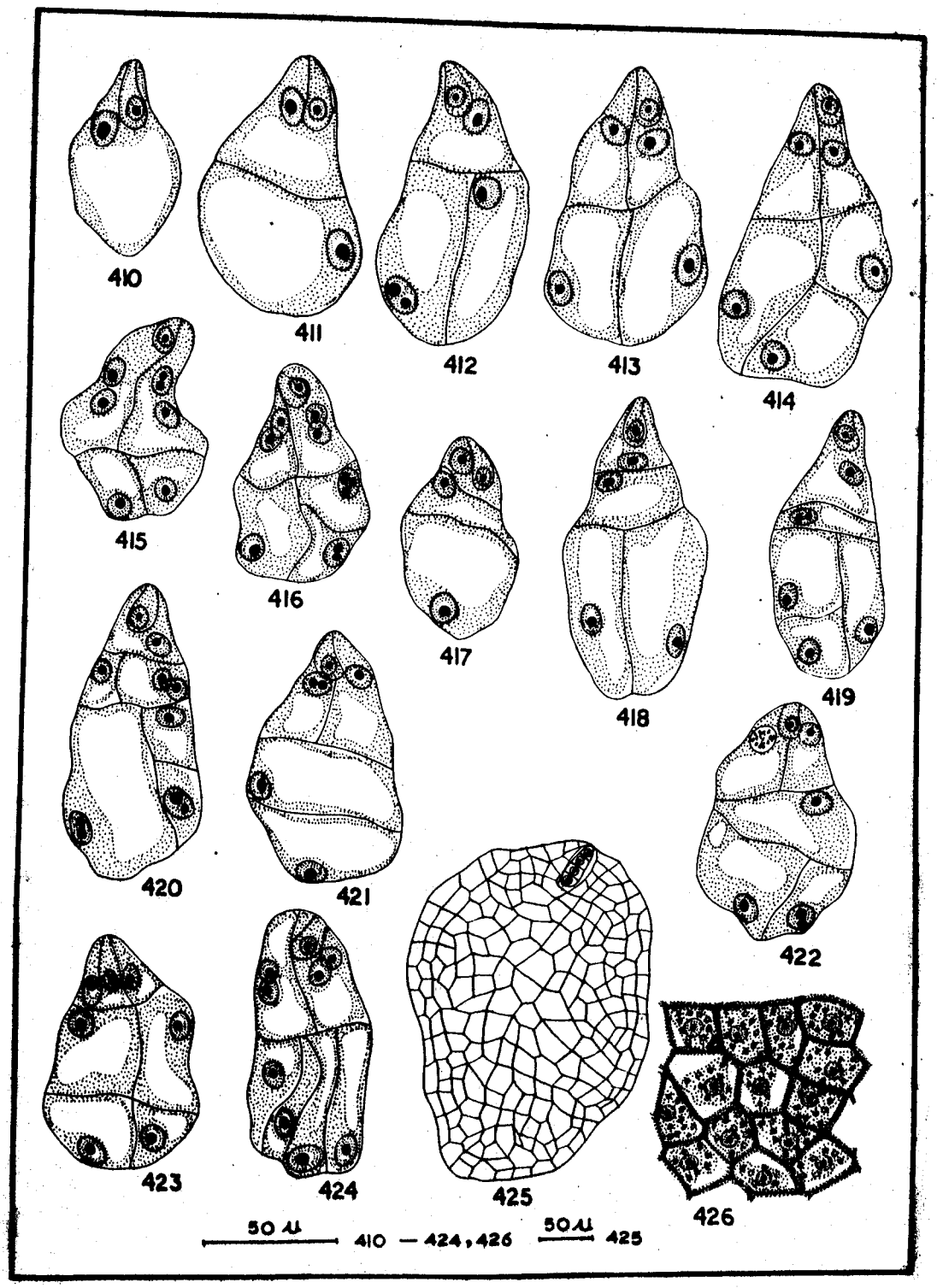
Explanation of figures

Figs.410–426. *S. khasianum*. Development of endosperm. Fig. 410. Fertilized embryo sac showing zygote and primary endosperm nucleus. Figs.411–413. 2,3 and 4-celled endosperm respectively. Figs.414–416. 5,6 and 7-celled endosperm respectively. Figs.417,418. 3 and 4-celled endosperm, the primary micropylar chamber has divided transversely. Fig.419. 5-celled endosperm, one of the two juxtaposed cells of chalazal chamber has divided transversely. Fig.420. 7-celled endosperm. Fig.421. 4-celled endosperm arranged in T-shaped manner. Figs.422,423. 5 and 6-celled endosperm. Fig.424. 8-celled endosperm, both the primary endosperm chambers have divided twice by vertical walls. Fig.425. Multicellular endosperm at linear proembryonic tetrad stage. Fig.426. Cells of mature endosperm with dense cytoplasm replete with starch grains.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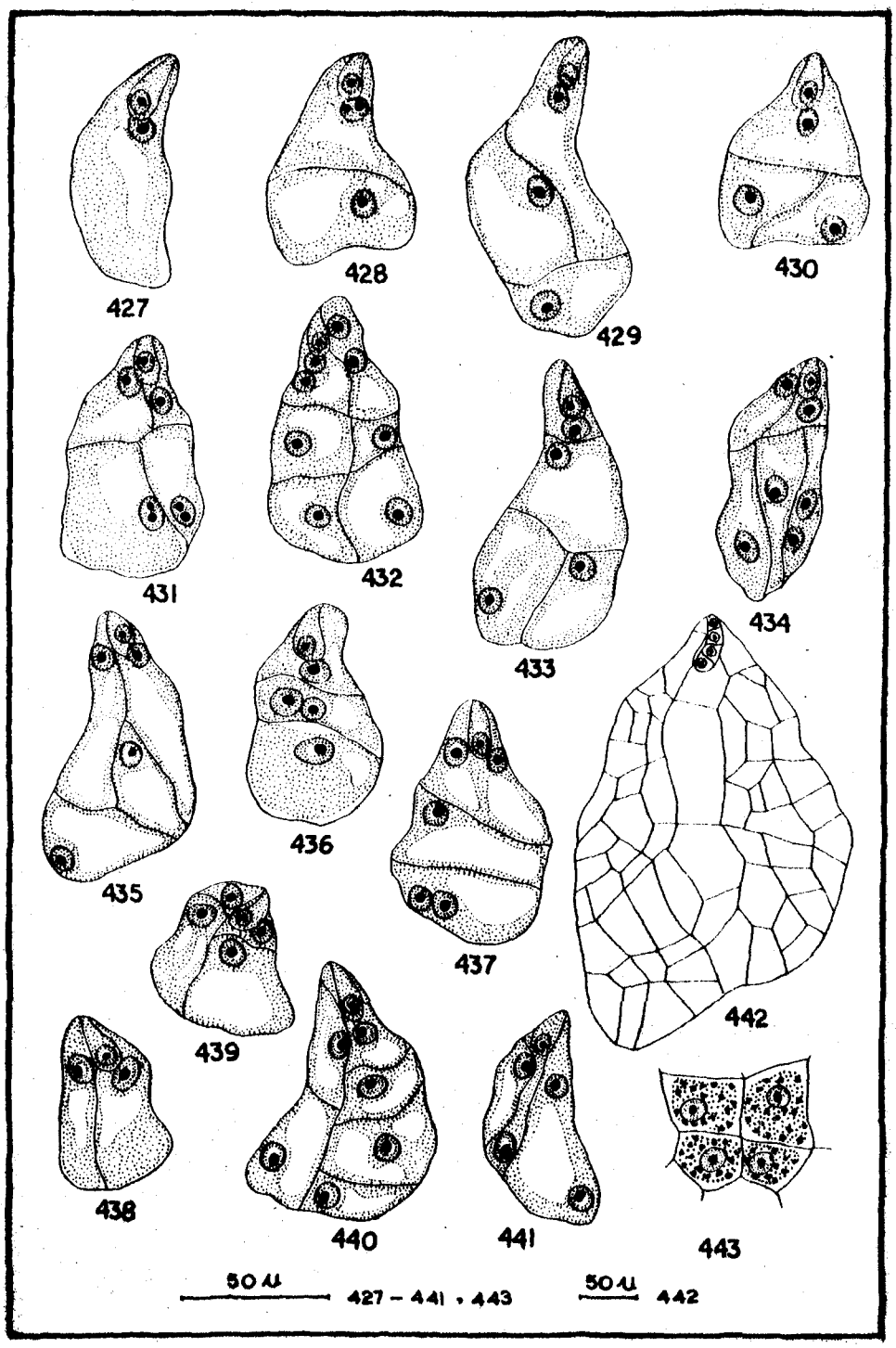
Explanation of figures

Figs.427–443. *S. sisymbrifolium*. Development of endosperm. Fig.427. Fertilized embryo sac showing zygote and primary endosperm nucleus. Fig.428. 2-celled endosperm. Figs.429, 430. 3-celled endosperm. Fig.431. 4-celled endosperm, both the primary endosperm chambers have divided vertically. Fig. 432. 8-celled endosperm. Fig.433. 4-celled endosperm arranged in inverted T-shaped manner. Fig.434. 6-celled endosperm, the two cells of chalazal chamber have divided vertically instead of transversely. Figs.435,436. 4-celled endosperm, the division in primary chalazal endosperm chamber is delayed. Fig.437. 5-celled endosperm. Figs.438–440. The first division in the primary endosperm cell has been vertical, later both the cells have divided transversely. Fig.441. 4-celled endosperm, first two divisions are vertical. Fig.442. Multicellular endosperm with 4-celled linear proembryo. Fig.443. Cells of mature endosperm with dense cytoplasm replete with starch grains.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EMBRYOGENY

The embryogeny in the species of *Solanum* is inconsistent. Beside normal type of embryogeny, sporadic variations which belong to the other principal type also may occur in the same species. Therefore, the embryogeny in the species described here has been dealt with separately.

S. aethiopicum

The division in the zygote is delayed unless sufficient amount of endosperm is formed.

The zygote divides transversely forming an apical cell *ca* and a basal cell *cb* (Figs.444,445). The cells *ca* and *cb* divide transversely producing the tiers *l*, *l'* and *m* and *ci* respectively (Figs.446,447). Thus at 4-celled stage the proembryo has linear disposition of its cells (Fig.447). The cell *ci* divides transversely forming *n* and *n'* (Fig.448). Later, the cells *l* and *l'* divide by vertical walls producing quadrant proembryo (Figs.449,450). Side by side *n* and *n'* divide transversely producing *h*, *k* and *o*, *p* respectively (Figs.449-451). The quadrant cells divide by vertical walls forming an octant proembryo (Figs.451-453). The cell *m* also divides vertically and contributes to the embryo proper (Figs.452,453). The derivatives of *n* and *n'* may divide transversely and form the suspensor (Figs.452-456). The cells of the suspensor may

divide longitudinally producing a biseriate suspensor (Figs. 453-455). Repeated divisions in the octant cells give rise to a globular proembryo (Figs.454-456), which subsequently differentiates into heart-shaped, torpedo and finally to a mature curved dicotyledonous embryo (Figs.458-460). The tiers l, l' and m contribute to the development of embryo proper while the derivatives of ci form a suspensor. Thus the embryogeny in S. aethiopicum conforms to the Myosotis variation of Chenopodiad type.

In an exceptional case a 10-celled proembryo appears to have developed from a T-shaped proembryonic tetrad and the embryogeny rarely may conform to the Onagrad type (Fig.457).

S. citrullifolium

The zygote divides transversely producing a terminal cell ca and a basal cell cb (Figs.461,462). The cells ca and cb divide transversely to give rise to l, l' and m and ci respectively (Figs.462-464). Thus four celled proembryo has linear disposition of its cells (Fig.464). The cells m and ci divide transversely producing d, f and n and n' respectively (Figs.465-469). These cells form the suspensor. The tiers l and l' divide vertically forming quadrant proembryo (Figs.466-468). The quandrant cells divide vertically forming octant proembryo (Figs.469-471). Later, the divisions in the derivatives of l and l' result in a globular proembryo (Fig.472-474).

The globular preembryo subsequently differentiates into heart-shaped (Figs.475), torpedo (Fig.476) and finally to a mature coiled dicotyledonous embryo (Fig.477).

Thus the embryogeny in S. citrullifolium conforms to the Nicotiana variation of Solanad type.

Rarely the cell m divides vertically and contributes to the embryo proper and thus the embryogeny may rarely conform to the Myosotis variation of Chenopodiad type.

Adventive embryony

In addition to the zygotic embryos a number of embryos develop from the endothelial cells. The endothelium differentiates at 2-nucleate embryo sac stage. After fertilization, it becomes 1-2 layered and its cells possess vacuolated cytoplasm (Figs.478-482). The differentiation of embryos from the cells of endothelium usually starts when sufficient amount of endosperm is formed (Fig.478). Any cell of endothelium may behave as embryo initial, which proliferates and divides to form a group of cells which eventually push their way into the embryo sac (Figs,478-482). In case where the endothelial embryos develop most of the endosperm is consumed (Figs.479-482). As a result the zygotic embryos or even the zygote degenerates (Fig.481). During the seed development it has also been observed that endothelial embryos degenerate. The degeneration of zygotic or endothelial embryos may be due to lack of

proper nutrition as endosperm does not develop further and is consumed by the endothelial embryos. Thus resulting seeds are abortive.

The number of embryos developing from the cells of endothelium is quite variable and sometimes they completely fill the embryo sac cavity (Figs.481,482). There is no definite sequence of the cell divisions in the embryos developed from endothelium. The origin of adventive embryos can be ascertained by their lateral position, lack of suspensor and the cell contents, which resemble to those of endothelial cells.

S. integrifolium

The zygote undergoes a short period of rest and divides by a transverse wall producing an apical cell ca and a basal cell cb (Figs.483,484). The cells ca and cb divide transversely producing the tiers l, l' and m and ci respectively (Figs.485,486). Thus a linear proembryonic tetrad is formed (Figs.486). The cell ci divides transversely producing n and n' (Fig.487). The cells n and n' again divide in the similar plane producing o, p and h, k respectively (Figs.488, 489), which constitute the suspensor of the embryo. The division in l may precede that in l' or vice-versa (Figs.490,491). The tiers l and l' divide vertically producing quadrant proembryo (Fig.492). The cell m also divides vertically and

contributes to the embryo proper (Figs.493-498). The quadrant cells divide vertically producing an octant proembryo (Figs. 494-496). Repeated divisions in the cells of octant and m result in a globular proembryo (Figs.498,499). The globular proembryo subsequently differentiates into heart-shaped (Fig. 505) and finally to mature slightly curved dicotyledonous embryo (Fig.506). Thus the embryogeny in S. integrifolium conforms to the Myosotis variation of Chenopodiad type. Occasionally the cell m contributes to the suspensor of the proembryo and the division in the cells of quadrant results in an octant proembryo (Figs.500-502). Thus the embryogeny occasionally may conform to Nicotiana variation of Solanad type.

Rarely the proembryonic tetrad is T-shaped (Fig.503) and the embryogeny may conform to Onagrad type.

Exceptionally cleavage of young proembryo has also been observed (Fig.504).

Variations in the curvature, size and number of cotyledons of the mature embryo have also been observed. In one exceptional case the curvature of the mature embryo is abnormal giving an S-shaped structure (Fig.507). In another case the two cotyledons are of unequal size (Fig.508). Still in another case there are three cotyledons (Fig.509).

S. khasianum

The zygote undergoes a period of rest and divides transversely producing a terminal cell ca and a basal cell cb (Figs.510,511). The division in ca and cb is transverse producing the cells l, l' and m and ci respectively (Figs.512, 513). Thus the 4-celled proembryo has linear disposition of its cells (Fig.513). The cell m divides transversely giving rise the cells d and f (Figs.514,515). The cell ci also divides in the similar plane producing the cells n and n' (Fig. 516). Later, the cells n and n' divide transversely producing the cells h, k & o,p respectively (Figs.517,518). The cells d, f, h, k, o, p constitute the suspensor of the embryo. The division in tier l precedes that in l' (Figs.519). The tier l and l' divide vertically producing quadrant proembryo (Fig.520). The derivatives of m and ci divide transversely forming a long suspensor (Fig.520). The cells of quadrant divide vertically producing octant proembryo (Fig.521). Repeated divisions in the octant cells result in a globular proembryo (Figs.522-524). The globular proembryo subsequently differentiates into heart-shaped, torpedo-shaped and finally to a mature coiled dicotyledonous embryo (Figs.525-527).

Thus the embryogeny in S. khasianum conforms to the Nicotiana variation of Solanad type.

S. nigrumbrifolium

The first division in the zygote is transverse producing a terminal cell ca and a basal cell cb (Figs.528,529). The cells ca and cb divide transversely to give rise to l, l' and m and ci respectively (Figs.530,531). Thus a linear proembryonic tetrad is formed (Fig.531). The cell m divides transversely forming d and f (Figs.532,533). The division in l precedes that in l' (Fig.534). The cells l and l' divide by vertical wall forming a quadrant proembryo (Fig.535). The quadrant cells divide vertically forming an octant proembryo (Fig.537). Side by side the cell ci also divides transversely producing the cell n and n' (Fig.537). The cells d, f, n and n' constitute the suspensor of the embryo. The cells of the suspensor sometimes may divide longitudinally producing a biseriate suspensor (Fig.539). Repeated divisions in the octant cells result in a globular proembryo (Figs.538,540,541), which subsequently differentiates into heart-shaped, torpedo-shaped and finally to a mature, coiled dicotyledonous embryo (Figs.542-544). Thus the embryogeny in S. nigrumbrifolium conforms to the Nicotiana variation of Solanad type.

Rarely the cell m divides longitudinally and contributes to the development of embryo proper (Fig.536). Thus the embryogeny rarely may conform to the Myosotis variation of Chenopodiad type.

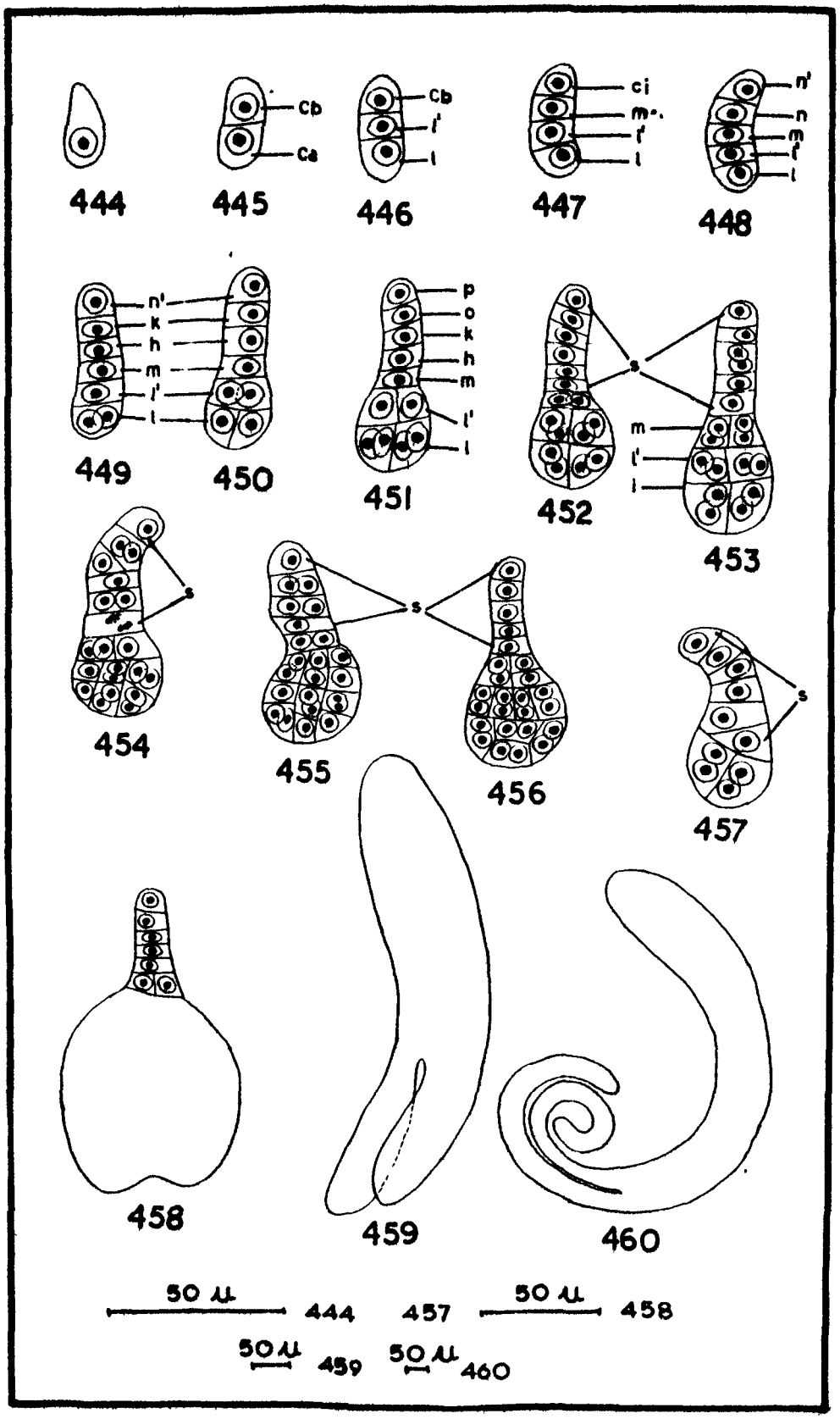
EMBRYOGENY

DISTINGUISHING CHARACTERS

Characters	S. aethiopicum	S. citrullifolium	S. integrifolium	S. khasianum	S. sisymbrifolium
Preembryonic tetrad	Linear	Linear	Linear Rarely T-shaped	Linear	Linear
Embryogeny Conforms	Usually Myosotis variation of Chenopodiad type, rarely Capsella variation of Onagrad type	Usually Nicotiana variation of Solanad type, rarely Myosotis variation of Chenopodiad type	Usually Myosotis variation of Chenopodiad type, occasionally Nicotiana variation of Solanad type, rarely Onagrad type	Usually Nicotiana variation of Solanad type	Usually Nicotiana variation of Solanad type, rarely Myosotis variation of Chenopodiad type
Polyembryony	Absent	Adventive embryos developed from endothelium	Cleavage pro-embryony present	Absent	Absent

Explanation of figures

Figs.444–460. *S. aethiopicum*. Embryogeny. Fig.444. Zygote. Fig.445. 2-celled proembryo. Fig.446. 3-celled proembryo. Fig.447. Linear proembryonic tetrad. Fig.448. 5-celled linear proembryo. Fig.449. 7-celled proembryo; the tier 1 has divided vertically. Fig.450. Quadrant stage. Fig.551. 11-celled proembryo. Figs.452,453. Octant stage; the cell m has divided vertically. Figs.454,455. Post octant stages. Fig.456. Globular proembryo. Fig.457. 10-celled proembryo developed from T-shaped proembryonic tetrad. Fig.458. Heart-shaped embryo. Fig.459. Torpedo-shaped embryo. Fig.460. Mature coiled dicotyledonous embryo.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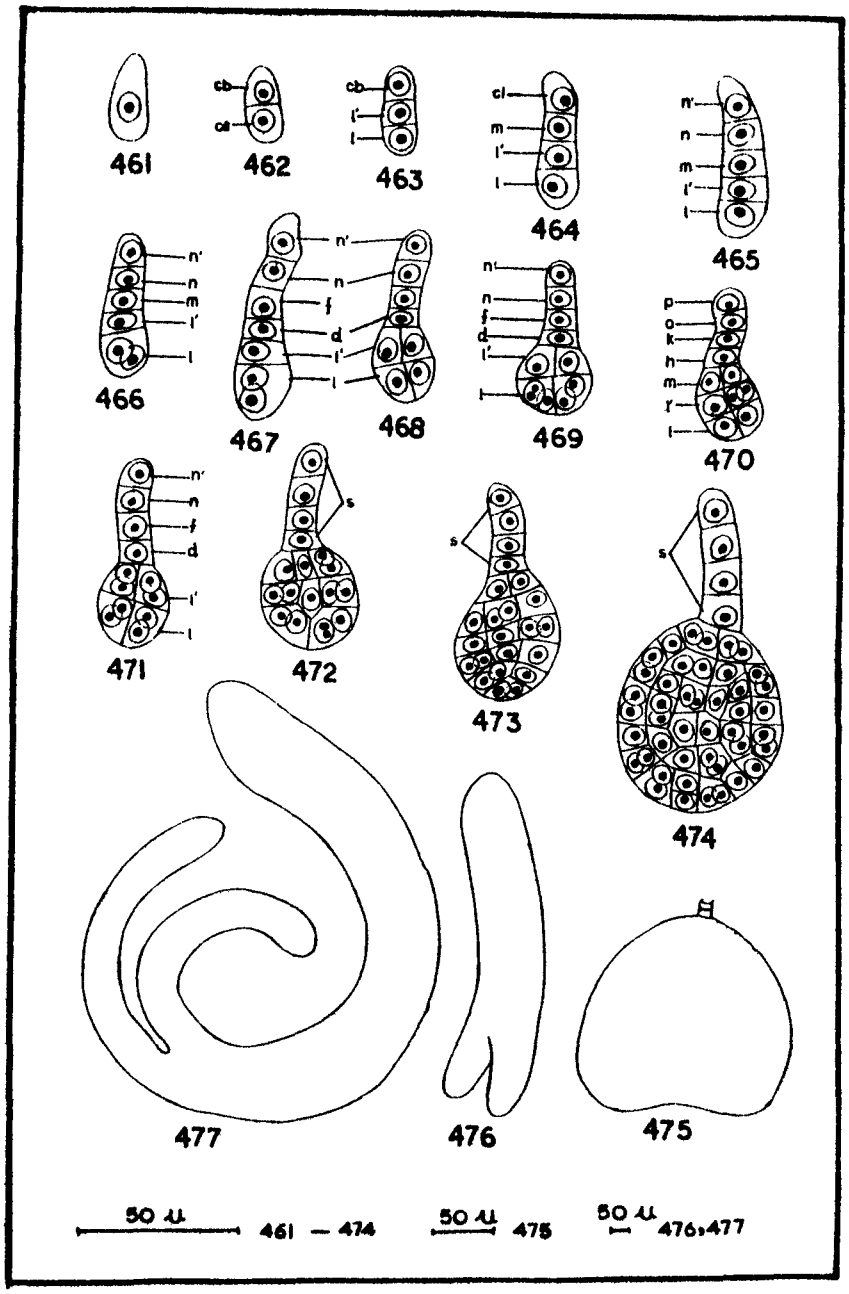
Explanation of figures

Figs.461-477. *S. citrullifolium*. Embryogeny. Fig.461. Zygote. Fig.462. 2-celled proembryo. Fig.463. 3-celled proembryo. Fig.464. Linear proembryonic tetrad. Fig.465. 5-celled linear proembryo. Figs.466,467. 6 and 7-celled proembryo respectively, the cell l has divided vertically. Fig.468. Quadrant stage. Fig.469. 10-celled proembryo. Fig.470. 11-celled proembryo, the cell m has divided vertically. Fig.471. Octant stage. Fig.472,473. Post octant stages. Fig.474. Globular proembryo. Fig.475. Heart-shaped embryo. Fig.476. Torpedo-shaped embryo. Fig. 477. Mature curved dicotyledonous embryo.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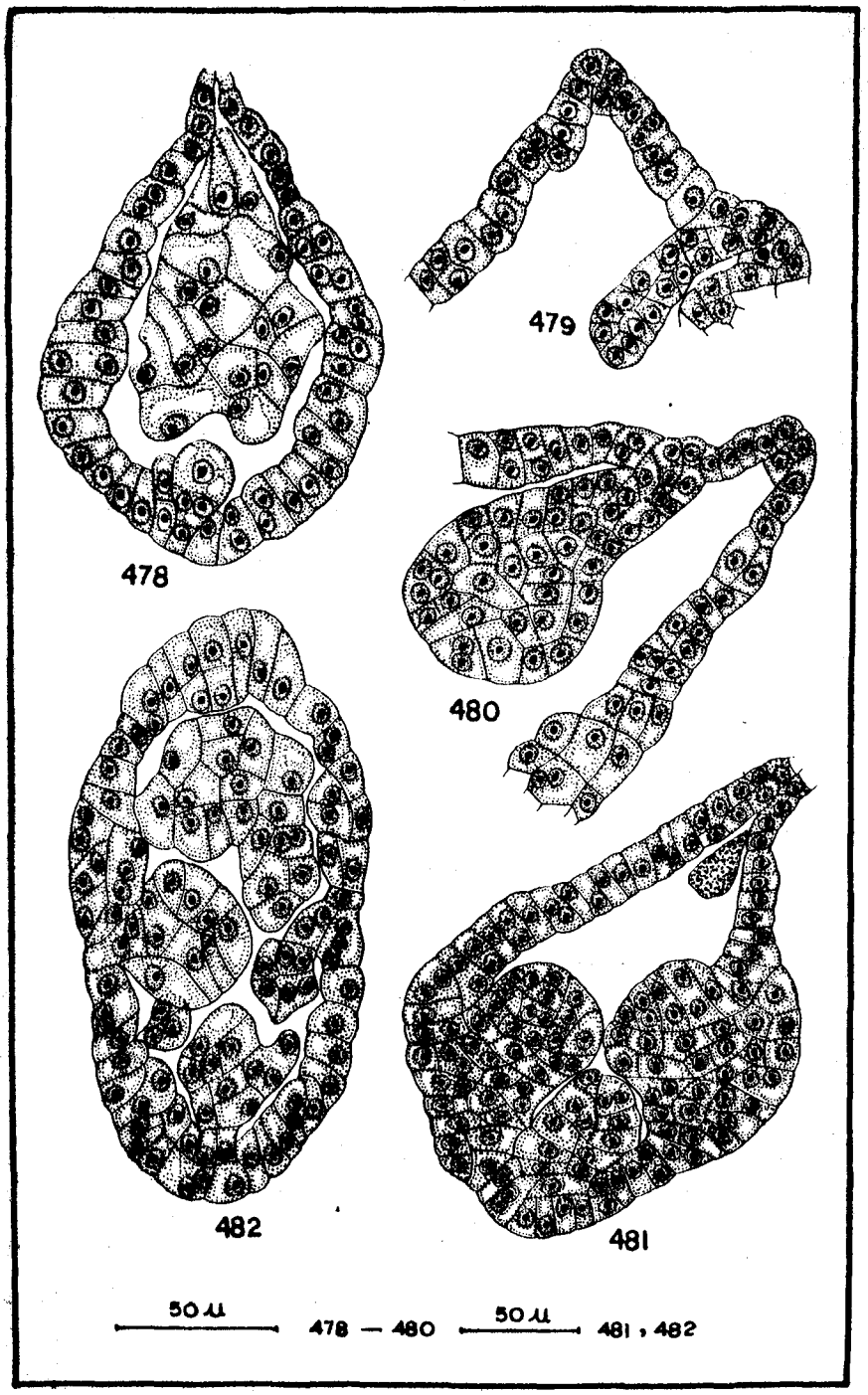
Explanation of figures

Figs.478–482. *S. citrullifolium*. Polyembryony. Fig.478. L. s. part of fertilized ovule showing zygote, cellular endosperm well developed endothelium and initiation of endothelial embryos towards chalazal side. Figs.479,480. Endothelium showing adventive embryos. Fig.481. L.s. fertilized sac showing endothelial embryos, the zygotic embryo is degenerating. Fig.482. L.s. fertilized sac, the embryo sac is almost filled up with endothelial embryos of different shapes and sizes.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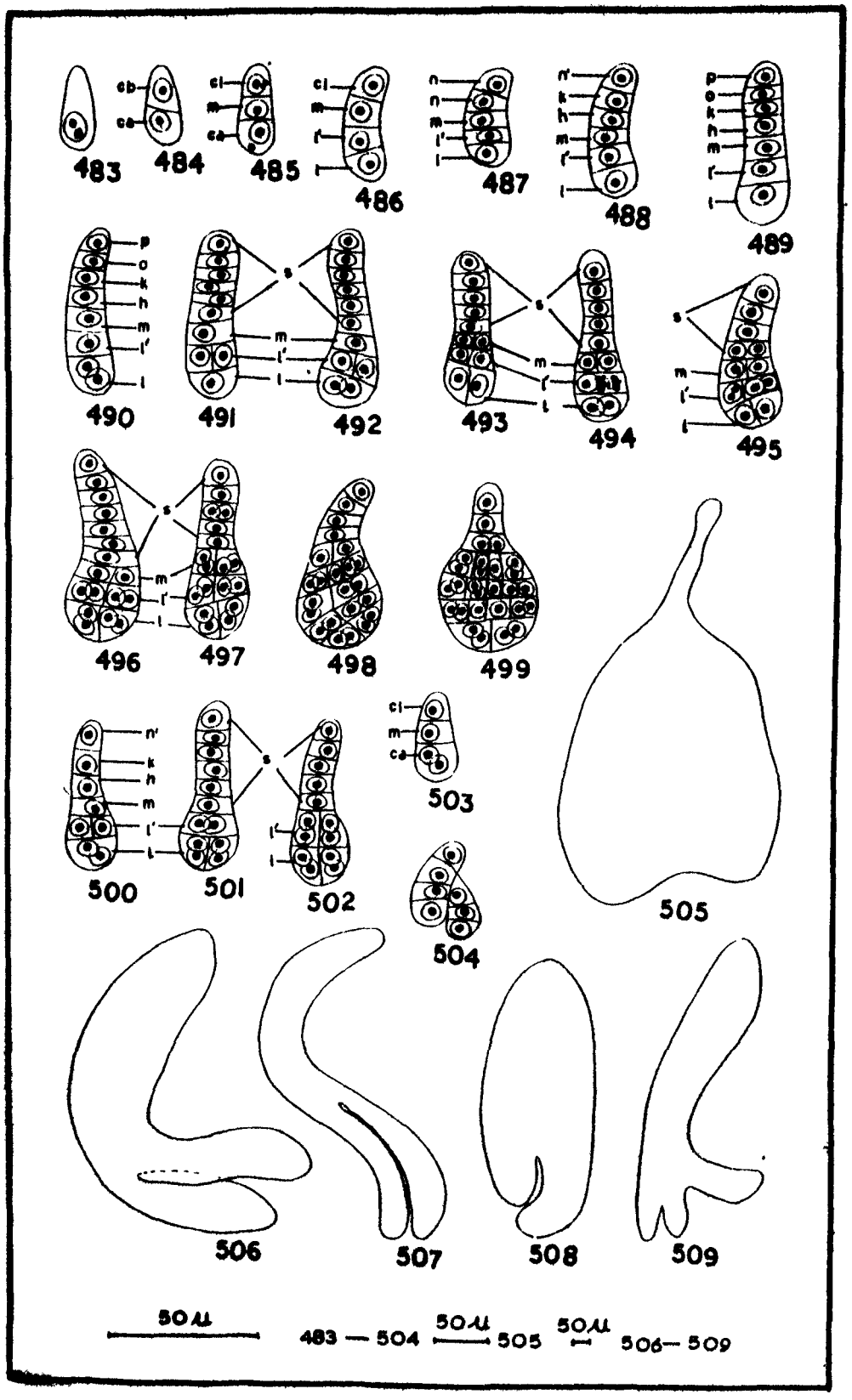
Explanation of figures

Figs.483–509. *S. integrifolium*. Embryogeny. Fig.483. Zygote. Fig.484. 2-celled proembryo. Fig.485. 3-celled proembryo, the cell *cb* has divided transversely producing *m* and *ci*. Fig.486. Linear proembryonic tetrad. Figs.487–489. 5,6 and 7-celled linear proembryos respectively. Fig. 490. 8-celled proembryo, the tier *l* has divided vertically. Fig.491. 10-celled proembryo, the tier *l'* has divided vertically. Fig.492. Quadrant stage. Figs.493,494. 11-celled proembryos, the cell *m* has divided vertically. Fig.495. 12-celled proembryo. Fig.496. Octant stage. Fig.497. 18-celled proembryo. Fig.498. Early globular stage. Fig.499. Globular proembryo. Fig.500. Quadrant stage. Fig.501. 12-celled proembryo, the tier *l* and *l'* have divided vertically. Fig.502. Octant stage. Fig.503. T-shaped proembryonic tetrad. Fig.504. Cleavage of proembryo. Fig.505. Heart-shaped embryo. Fig.506. Mature slightly curved embryo. Fig.507. Mature embryo showing abnormal S-shaped curvature. Fig.508. Mature embryo with unequal cotyledons. Fig.509. Mature embryo with three cotyledons.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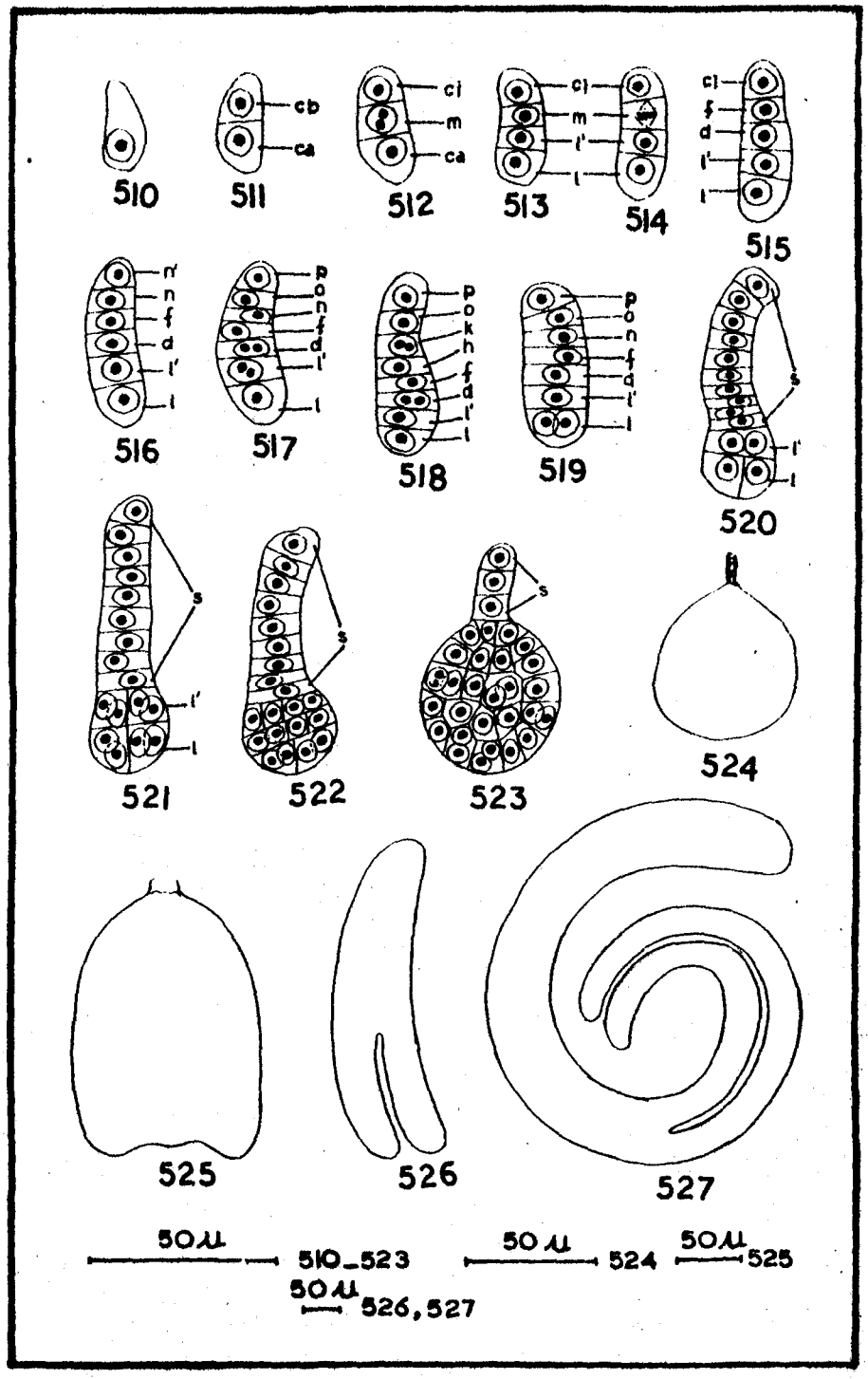
Explanation of figures

Figs.510-527. *S. khasianum*. Embryogeny. Fig.510. Zygote. Figs.511,512. 2 and 3-celled proembryos respectively. Fig. 513. Linear proembryonic tetrad. Figs.514,515. 4 and 5-celled linear proembryos respectively. Figs.516-518. 6,7 and 8-celled linear proembryos respectively. Fig.519. 8-celled proembryo, the tier $\frac{1}{4}$ has divided vertically. Fig. 520. Quadrant stage. Fig.521. Octant stage. Fig.522. Post octant stage. Figs.523,524. Globular proembryos. Fig.525. Heart-shaped embryo. Fig.526. Torpedo-shaped embryo. Fig.527. Mature coiled dicotyledonous embryo.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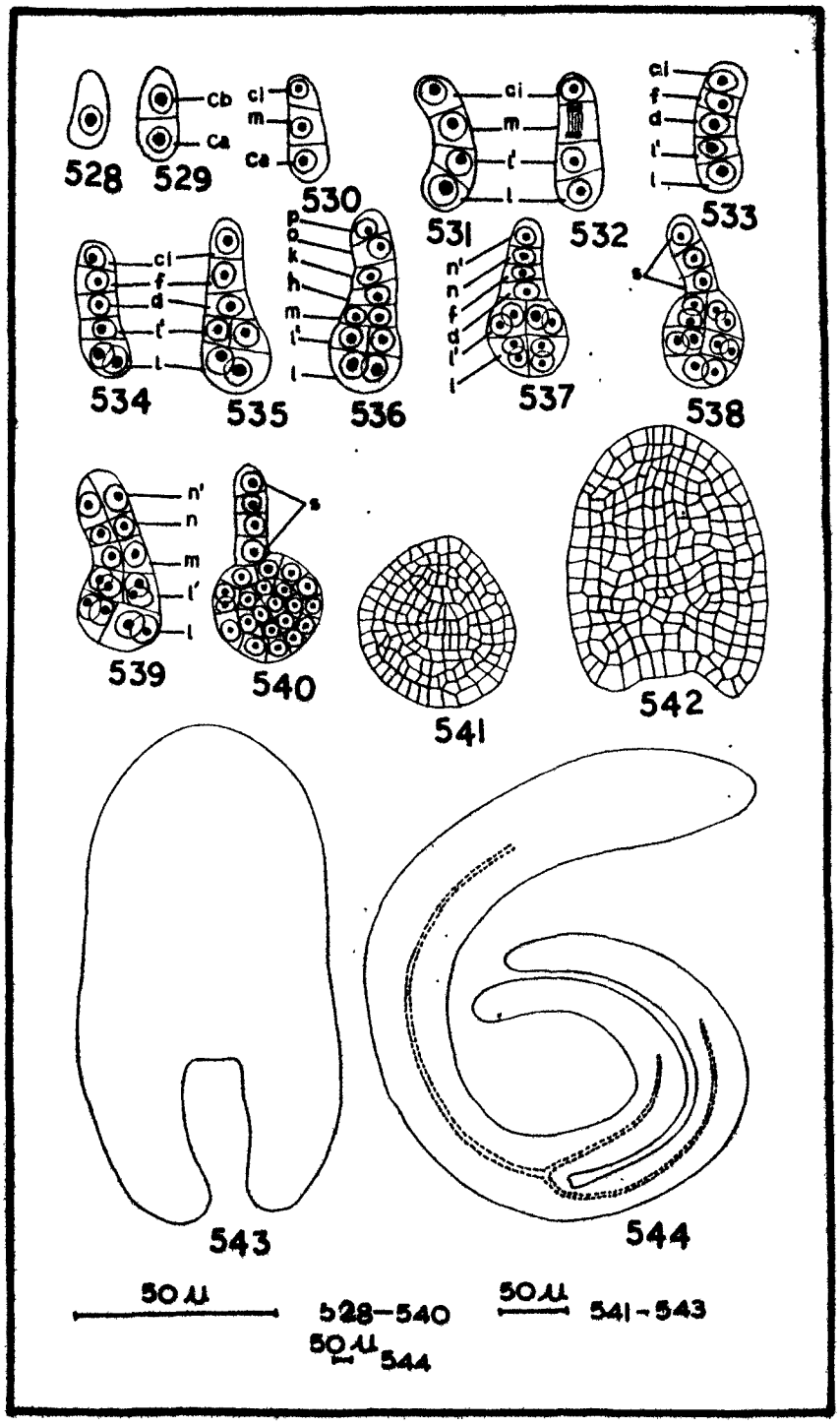
Explanation of figures

Figs.528-544. *S. sisymbrifolium*. Embryogeny. Fig.528. Zygote. Fig.529. 2-celled proembryo. Fig.530. 3-celled proembryo. Fig.531. Linear proembryonic tetrad. Fig.532. 4-celled linear proembryo; the cell m is dividing transversely. Fig.533. 5-celled linear proembryo. Fig.534. 6-celled proembryo; the tier l has divided vertically. Fig. 535. Quadrant stage of proembryo. Fig.536. 10-celled proembryo; the tier m has divided vertically. Fig.537. Octant stage. Fig.538. Post octant stage of proembryo. Fig.539. 14-celled proembryo; the cells m, n and n' have divided vertically. Figs.540,541. Globular proembryos. Fig.542. Heart-shaped embryo. Fig.543. Torpedo-shaped embryo. Fig. 544. Mature coiled dicotyledonous embryo.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SEED

The ovules are anatropous, unitegmic and tenuinucellate in the species described here. The integument at the time of initiation is few celled thick. At the mature embryo sac stage it becomes 7-9 celled thick on the free side in *S. aethiopicum* and *S. citrullifolium* and 7-8 celled thick in *S. integrifolium*, *S. khasianum* and *S. sisymbrifolium*. The innermost layer of the integument differentiates as endothelium during the female gametophyte development. Endothelium usually degenerates during the seed maturity except in *S. sisymbrifolium*, where it persists and forms the innermost layer of the seed coat.

However, considerable differences in the development and structure of seeds have been observed in the species described here. Therefore for the sake of clarity the development of seed has been dealt-with separately.

S. aethiopicum

The cells of the integument after fertilization divide more rapidly and even at zygote stage it becomes 18-20 celled thick (Fig.545). The endothelial cells are radially elongated and possess vacuolated cytoplasm (Fig.545). The divisions in the cells of middle layers of the integument continue and at globular proembryo stage it becomes 22-26 celled (Fig.546). At this

stage the endothelium starts degeneration and fibrous thickenings develop in the cells of epidermis (Fig.546). The developing endosperm encroaches upon the cells of the integument, thus at maturity the cells of integument are completely consumed except the epidermis. Concurrently the epidermal cells enlarge, become heavily lignified and show sclerotic thickenings in the inner portion and fibrous thickenings in the outer region (Fig.548). Most of the endosperm is consumed by the developing embryo and only few layers persist in the mature seed (Fig.548). Anatomically the mature seed comprises an epidermis, persistent endosperm and coiled dicotyledonous embryo (Fig.547). The epidermis is the main mechanical layer and constitutes the seed coat (Fig.548).

The seeds are endospermic. The cells of the endosperm at mature seed stage possess dense cytoplasm replete with starch grains. Cellulosic thickenings are also deposited on the walls of endosperm cells (Fig.548).

Morphologically the mature seeds are small, flat and of light cream colour.

S. citrullifolium

After fertilization repeated divisions occur in the cells of the middle layers of the integument, thus it becomes 8-11 celled thick at zygote stage (Fig.549). The endothelial

cells are radially elongated with vacuolated cytoplasm (Fig. 549). It is single layered, occasionally at places it becomes 2-layered. Its cells may proliferate and form the adventive embryos, which fill the embryo sac cavity. The divisions in the cells of integument continue and it becomes 17-20 celled thick at globular proembryo stage (Fig.550). The cells of the epidermis enlarge considerably and their radial and inner tangential walls become lignified (Fig.550). The endothelium starts degeneration at this stage. The developing endosperm exerts a pressure on the cells of the integument and as a result the number of cell layers of the integument is reduced to 14-16 layered at heart-shaped embryo stage (Fig.551). The cells of the epidermis become highly lignified (Fig.551). The degeneration of the cells of the integument continues and at torpedo-stage 6-9 cell layers are left (Fig.552). During the further development the cell layers of the integument are totally absorbed.

Anatomically the seed comprises an epidermis, persistent endosperm and coiled dicotyledonous embryo (Fig. 553,554). Epidermis is the main mechanical layer and constitutes the seed coat. Its cells develop sclerotic thickenings in the inner portion and rod like thickenings in the outer region (Fig.555). The cells of the endosperm are rich in reserve food.

In the mature seed the endosperm extends between the coiled embryo and this part of the endosperm is characterized by a bulbous comma head and a slender comma stem.

The mature seeds are small and black in colour with rough surface.

S. integrifolium

The number of cell layers of the integument increases after fertilization and becomes 20-22 celled thick at the zygote stage (Fig.556). The number of cell layers of integument becomes maximum (30-35) at globular proembryo stage (Figs.557). The endothelium persists upto the globular proembryo stage (Figs.556, 557). Its cells are almost isodiametric and possess vacuolated cytoplasm (Figs.556,557). Side by side the cells of the epidermis also develop fibrous thickenings on their radial walls (Fig.557). During the maturity of seed the cells of the integument are destroyed due to the pressure exerted by the developing endosperm. The endothelium degenerates at heart-shaped embryo stage. The seed coat at this stage comprises a highly lignified epidermis and 10-12 cell layers of the integument (Fig.558). The degeneration of the integumental cells continues and in a completely mature seed only the epidermis of the integument persists. Thus anatomically the mature seed comprises an epidermis, persistent endosperm and mature curved dicotyledonous embryo (Fig.559). The epidermis is the main mechanical layer

and constitutes the seed coat (Fig.560). Its cells possess dense sclerotic thickenings in the inner portions and rod like projection in the outer portion (Figs.559,560). In the mature seed the endosperm cells possess dense cytoplasm replete with starch grains (Fig.560).

Mature seeds are small, flat and of light cream in colour.

S. khasianum

In fertilized ovules the number of cell layers of the integument increases and becomes 7-11 at zygote stage (Fig.561). The endothelial cells are either radially elongated or isodiametric and possess vacuolated cytoplasm (Fig.561). The divisions in the cells of the middle layers of the integument continue and at proembryonic tetrad stage the integument becomes 14-17 celled thick (Fig.562). The endothelium remains healthy upto this stage (Fig.562). During further development the endothelium degenerates.

The cells of the developing endosperm encroach upon the integumental cells, thus the cells lying adjacent to the endosperm are crushed and absorbed. Thus at heart and torpedo-stage of the embryo the integument is composed of 10-12 and 7-8 cell layers respectively (Figs.563,564). The thickenings in the epidermal cells become more pronounced and reach the outer

tangential walls (Figs.563,564). The cells of the integument are totally absorbed in the mature seed, thus anatomically the seed comprises an epidermis, persistent endosperm and mature coiled dicotyledonous embryo (Fig.565). Epidermis is the main mechanical layer and constitutes the seed coat. Its cells possess sclerotic thickenings in the inner portion and extend upto the outer tangential walls (Figs.565,566). The endosperm cells become rich in reserve food material and develop cellulosic thickenings on their walls. The endosperm extends between the coiled embryo and this part of the endosperm is characterized by a bulbous comma head and a slender comma stem.

Mature seeds are small, kidney shaped, flat, light brown in colour with smooth surface.

S. sisymbrifolium

After fertilization repeated divisions occur in the middle layers of the integument, thus the integument becomes 9-12 celled thick at zygote stage (Fig.567). The divisions in the cells of integument continue and at proembryonic tetrad stage it becomes 14-18 celled thick (Fig.568). In the early stages of seed development the endothelial cells are radially elongated, possessing dense cytoplasm and prominent nuclei (Fig.567). Later, the cells lose their contents and their walls become heavily lignified (Fig.571). At proembryonic tetrad stage the epidermal cells are considerably large and

fibrous thickenings develop on their radial walls (Fig.568). The developing endosperm encroaches upon the cells of the integument and thus the cells lying just out-side the endothelium are absorbed and their absorption progresses from inside to out-side. At heart-shaped embryo stage integument consists of 8-11 cell layers (Fig.569). At this stage the cells of the integument lying out side the endothelium become tangentially flattened due to the pressure exerted by the developing endosperm cells (Fig.569). The lignification of the epidermal cells progresses from inner tangential walls to outer tangential walls (Fig.569).

In a completely mature seed the middle layers of the integument are totally absorbed, thus anatomically the seed comprises an epidermis, persistent thick walled endothelium, endosperm and mature coiled dicotyledonous embryo (Fig.570).

Epidermis becomes heavily lignified and along with the thick-walled endothelium it forms the seed coat (Fig.571). In the mature seed the endosperm extends between the coiled embryo and this part of endosperm is characterized by a bulbous comma head and a slender comma stem.

The mature dry seeds are small, flat, kidney shaped and light cream to brown in colour.

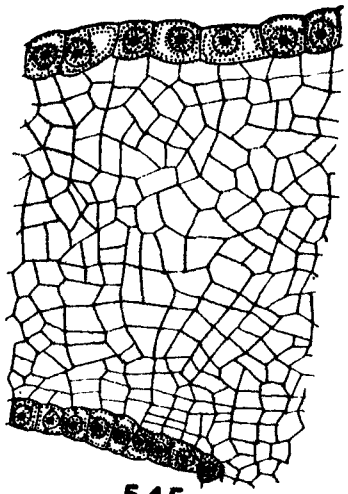
SEED

DISTINGUISHING CHARACTERS

Characters	*S. aethiopicum*	*S. citrullifolium*	*S. integrifolium*	*S. khasianum*	*S. sisymbrifolium*
External Morphology	Light cream, small flat with smooth surface	Black, small, with rough surface	Light cream, compressed with smooth surface	Light brown, kindney shaped with smooth surface	Light cream to light brown flat with smooth surface
Seed Comprises	Seed coat, endosperm and embryo	Seed coat, endosperm and embryo	Seed coat, endosperm and embryo	Seed coat, endosperm and embryo	Seed coat, endosperm and embryo
Seed Coat Comprises	Epidermis	Epidermis	Epidermis	Epidermis	Epidermis and lignified endothelium

Explanation of figures

Figs.545–548. *S. aethiopicum*. Development of seed. Fig.545. L.s. part of ovule at zygote stage showing 20,22-cell layers of integument, endothelial cells have vacuolated cytoplasm. Fig. 546. L.s. part fertilized ovule at globular proembryo stage showing 22–24 cell layers of integument. Fig.547. L.s. of mature seed showing epidermis, endosperm and mature coiled dicotyledonous embryo. Fig.548. L.s. part of mature seed showing thickenings in the epidermis and thick walled endosperm.



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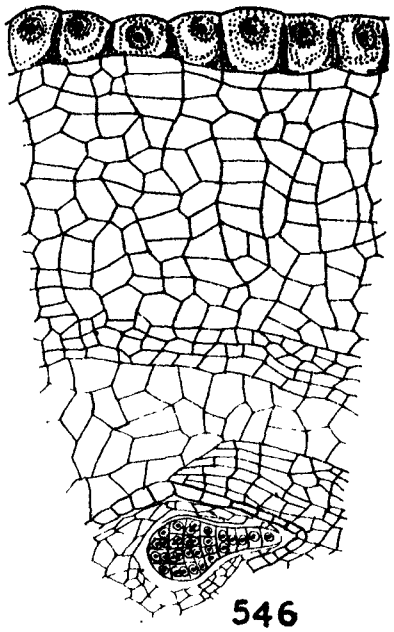

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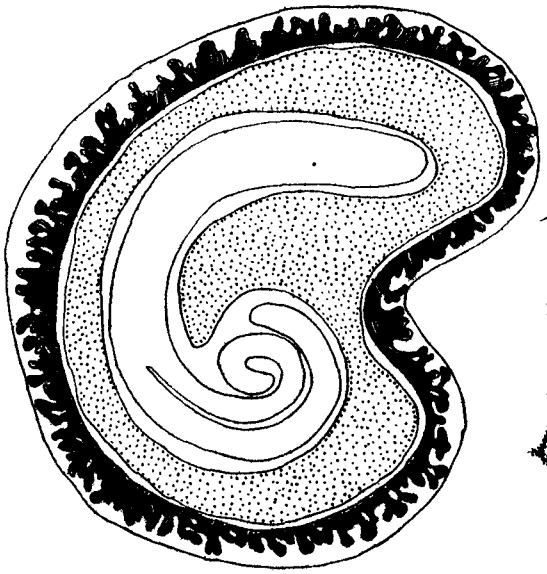

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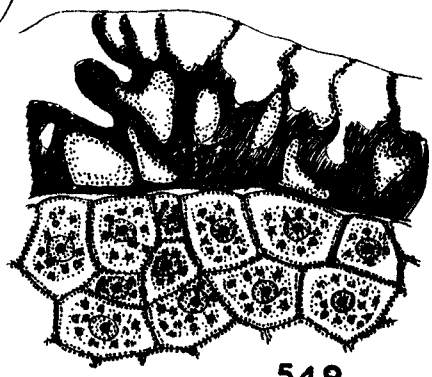

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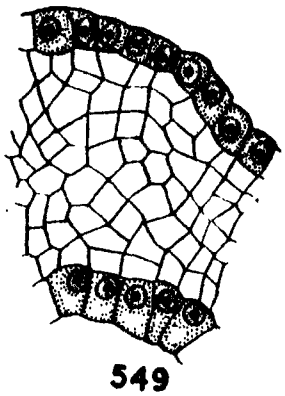
Explanation of figures

Figs.549-555. *Sa. citrullifolium*. Development of seed. Fig. 549. L.s. part of fertilized ovule at zygote stage showing 8-11-celled thick integument. Fig.550. L.s. part of fertilized ovule at globular proembryo stage showing 17-20-celled thick integument, endothelium, endosperm, globular proembryo and thickenings in the epidermal cells. Fig.551. L.s. part of seed at Heart-shaped embryo stage showing 14-16-celled thick integument and lignified epidermis. Fig.552. L.s. part of seed at torpedo-shaped embryo stage showing 7-9-celled thick integument, endosperm and lignified epidermis. Figs. 553,554. L.s. and v.s. of mature seeds respectively showing an epidermis, endosperm and embryo. Fig.555. L.s. part of mature seed showing epidermis, degenerated mass of integument cells and endosperm. The epidermal cells possess sclerotic thickenings in the inner portion and rod like fibrous thickenings in the outer region.



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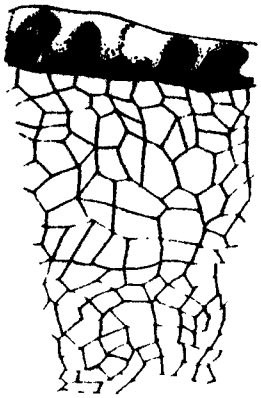

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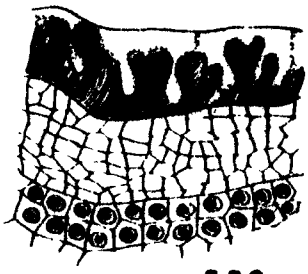

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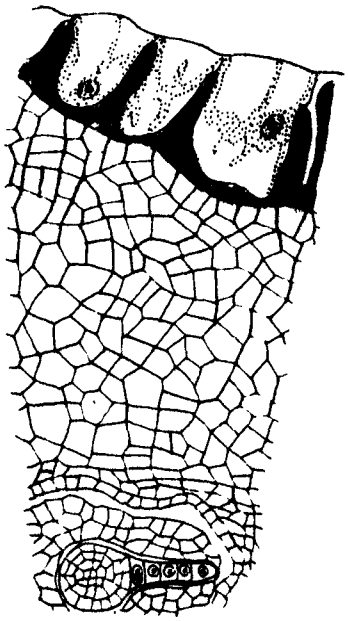

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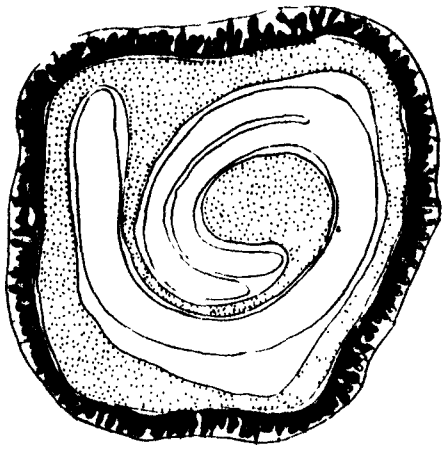

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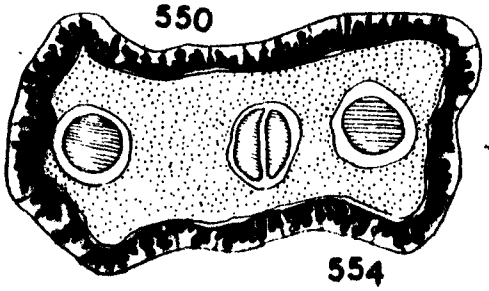

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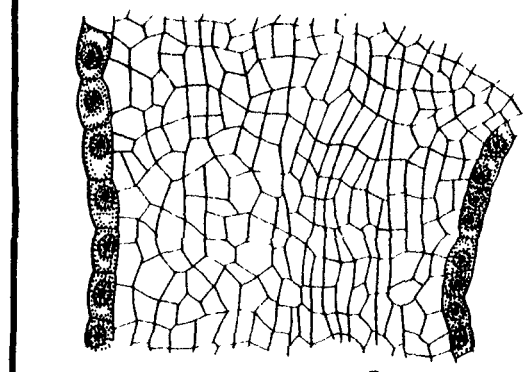
Explanation of figures

Figs.556-560. *S. integrifolium*. Development of seed. Fig. 556. L.s. part of ovule at zygote stage showing 20-22 layered thick integument. Fig.557. L.s. part of seed at globular proembryo stage showing 30-36 layered thick integument, endothelium, endosperm and globular proembryo. Thickenings have developed in the cells of epidermis. Fig.558. L.s. part of seed at torpedo-stage of embryo showing 10-12 celled thick integument, fibrous thickenings are well developed in the cells of epidermis. Fig.559. L.s. of mature seed showing lignified epidermis, endosperm and curved dicotyledonous embryo. Fig. 560. L.s. part of mature seed showing epidermis and thick walled endosperm. The epidermal cells possess sclerotic thickenings in the inner portion and rod like fibrous thickenings in the outer region.



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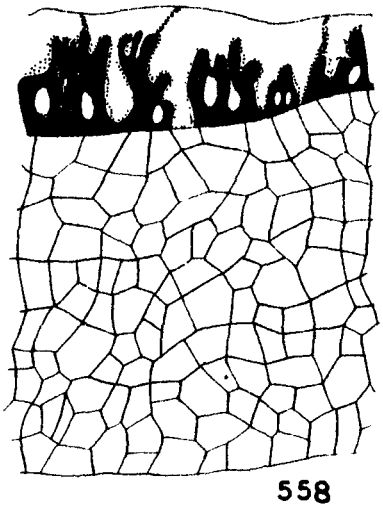

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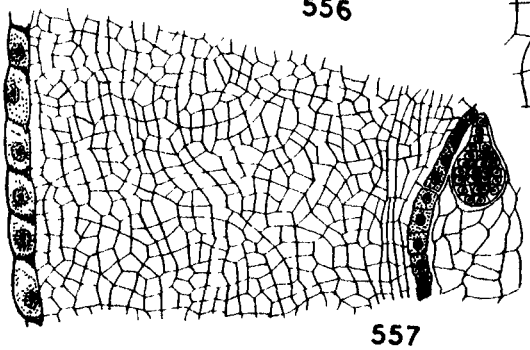

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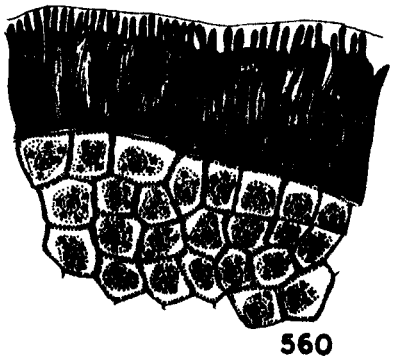

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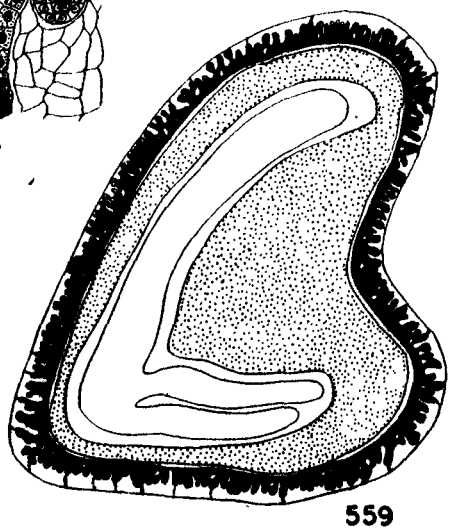

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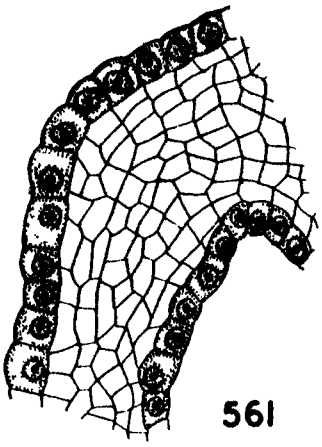
Explanation of figures

Figs.561-566. *S. khasianum*. Development of seed. Fig.561. L.s. part of ovule at zygote stage showing 8-11 celled thick integument. Fig.562. L.s. part of ovule at linear proembryonic tetrad stage showing 14-17 celled thick integument and endosperm. The fibrous thickenings are seen on the radial walls of the epidermal cells. Fig.563. L.s. part of seed at heart-shaped embryo stage showing 10-12 celled thick integument and thickenings in the epidermis. Fig.564. L.s. part of seed at torpedo-stage of embryo showing 7-8 celled thick integument, endosperm and thickenings in the epidermis. Fig.565. L.s. of mature seed showing lignified epidermis, endosperm and mature coiled dicotyledonous embryo. Fig.566. L.s. part of mature seed showing thickenings on the radial as well as inner and outer tangential walls of the epidermal cells and thick walled endosperm.



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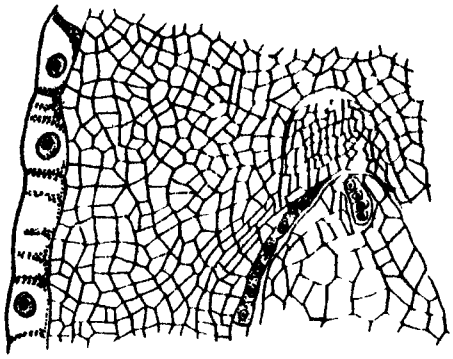

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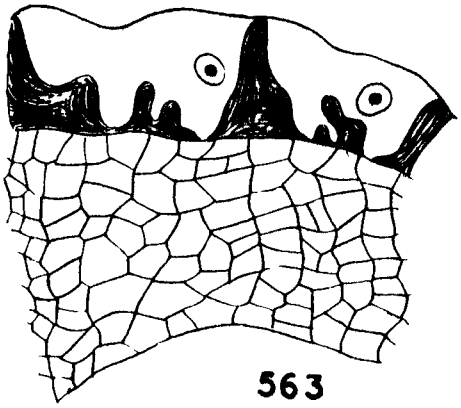

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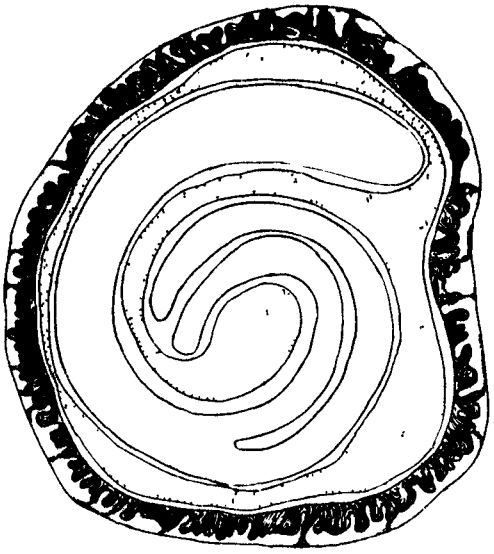

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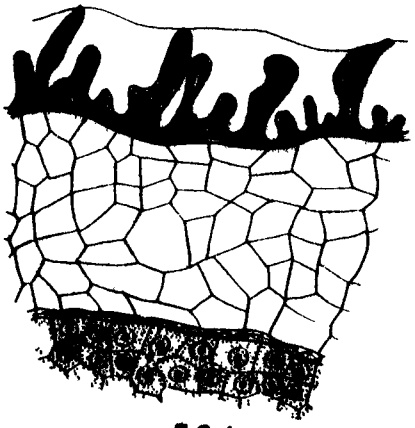

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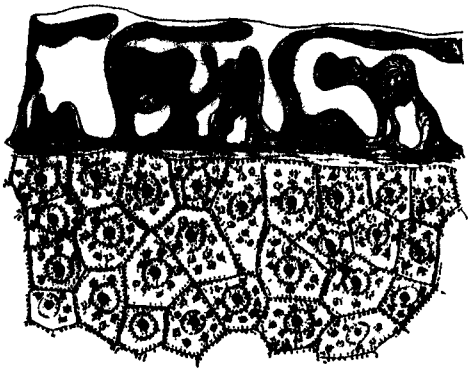

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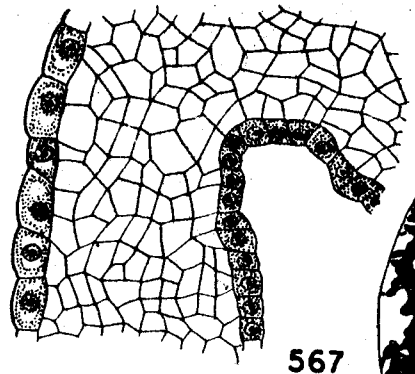
50μ 561 50μ 562-564, 566 50μ 565

Explanation of figures

Figs.567-571. *S. sisymbrifolium*. Development of seed. Fig. 567. L.s. of ovule at zygote stage showing 9-12 celled thick integument. Fig.568. L.s. part of ovule at linear proembryonic tetrad stage showing 15-20 celled thick integument and endothelium. Fibrous thickenings are seen on the radial walls of epidermal cells. Fig.569. L.s. part of seed at heart-shaped embryo stage showing 8-10 celled thick integument, persistent endothelium, few layers of endosperm and heart-shaped embryo. Fibrous thickenings are well developed in the epidermis. Fig. 570. L.s. of mature seed showing lignified epidermis, persistent endothelium, endosperm and mature coiled dicotyledonous embryo. Fig.571. L.s. part of mature seed showing lignified epidermis, persistent thick walled endothelium and endosperm.



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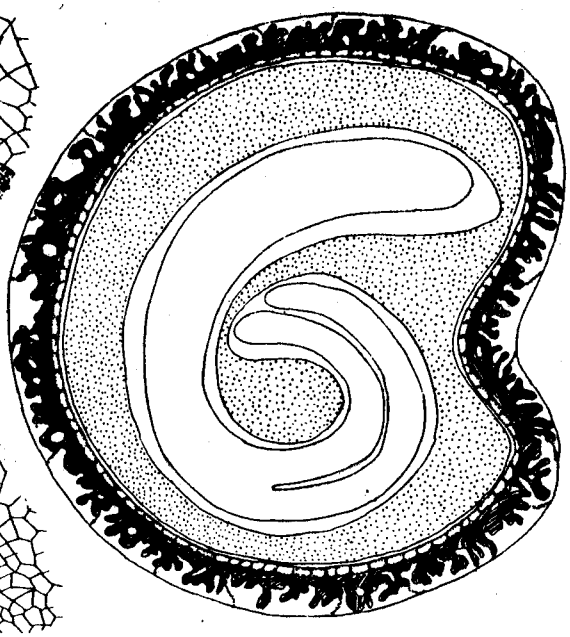

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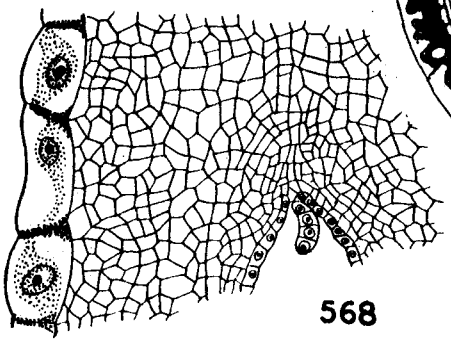

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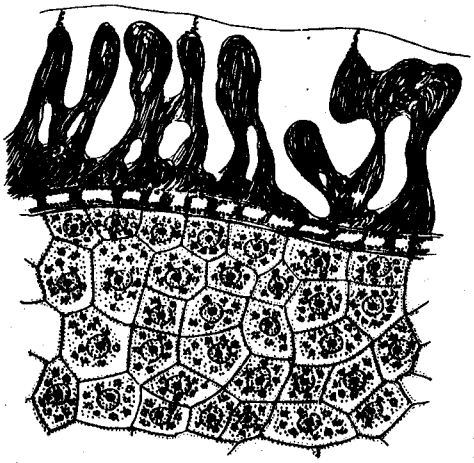

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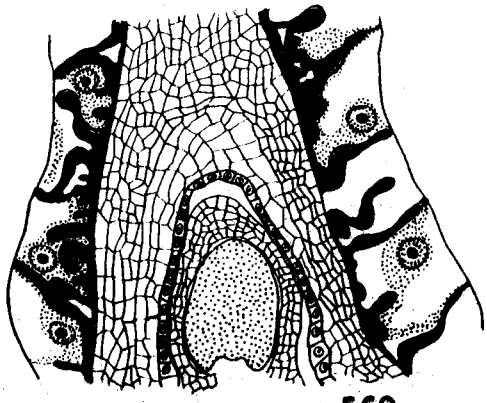

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DISCUSSION

The present discussion is confined to the interesting embryological features of the investigated species of Solanum as well as some general remarks about the order Tubiflorae. Some of the embryological characters appear to be important in determining the position of the genus itself while others appear to be helpful in this respect for the entire family.

In Tubiflorae the flowers are bisexual, actinomorphic, often zygomorphic, tetracyclic and hypogynous. In the primitive members the flowers are actinomorphic, tetracyclic and isostamenous, while in highly evolved ones they are zygomorphic with reduced number of stamens, carpels, placenta and ovules. From the regular isostamenous flowered families several lines of specialization are discernible. In polemoniaceae the flowers are pentamerous, regular with tricarpellary or sometimes bicarpellary ovary. The number of ovules varies from numerous to solitary in each chamber; the position of micropyle resembles that of Convolvulaceae. Hydrophyllaceae recall polymoniaceae in the plan of regular flower but the ovary is usually bicarpellary and bilecular. In Verbenaceae and Labiatae the number of stamen and number of ovules per carpel is reduced. The other line of evolution is seen in the sub order Solaneae. In Nolanaceae all the five stamens are of equal length and fertile, the ovary is pentacarpellary, 5-10 locular with many ovules in each locule. It is closely allied to Solanaceae,

where the flowers are pentamerous, actinomorphic, isostamenous with bicarpellary ovary. A tendency towards the production of fertile stamen with unequal length is found in tribe Salpiglossideae. In some of its genera the irregularity of corolla resembles Scrophulariaceae. Passing through Scrophulariaceae, the evolutionary tendency leads to a number of closely allied families, viz., Orobanchaceae, Gesneriaceae, Lentibulariaceae and Globulariaceae. Among this evolutionary line the reduction in the number of stamen is a normal feature. The presence of only two stamens in Lentibulariaceae shows extremely reduced condition. The ovary is bicarpellary or 2-1 locular. Sometimes the reduction in the number of ovules is discernible, although polyspermous ovary occurs in overwhelming majority.

The embryological features in different families of the order Tubiflorae reveal remarkable similarities. The tapetum is glandular.The pollen grains are 2-3 nucleate at the shedding stage. Deshiscence of the anther may be porous as well as longitudinal. The ovules are usually anatropous, unitegmic and tenuinucellate. Single celled female archesporium is hypodermal in origin and directly functions as megaspore mother cell. The development of female gametophyte conforms to the Polygonum type. The development of endosperm is variable and is of considerable phylogenetic significance. In the supposedly primitive families (Polymoniaceae and Convolvulaceae including Cuscuta) the endosperm is Nuclear. In Solanaceae, Hydrophyllaceae and Boraginaceae the endosperm may be Nuclear, Cellular or a type

intermediate between them. The condition in Boraginaceae is most remarkable, where all the three types of endosperm occur. In advance families the endosperm is Cellular, which is divisible into two main types depending upon the sequence of early cell divisions and differentiation of haustoria showing distinctive evolutionary sequence. This is well demonstrated in Scrophulariaceae (Glišić, 1936-37; Krishana Iyengar, 1940a, 1940b; Crété, 1951; Banerji, 1961). The embryogeny in the Tubiflorae usually conforms to the Onagrad type, but other types also may occur frequently. The interesting variations in the embryology of investigated species of Solanum and the light which these throw on the evolutionary tendencies in its species have been discussed below.

The organogeny takes place in acropetal succession in the investigated Solanaceae.

Davis (1966) classified four types of anther wall development in her book entitled, "Systematic embryology of the Angiosperms" and mentioned usually Dicotyledonous and rarely Basic types of anther wall development in Solanaceae.

The development of anther wall layers in Solanum aethiopicum, S. citrullifolium, S. integrifolium and S. glaucifolium conforms to the Dicotyledonous type and Basic type in S. khasianum. Dicotyledonous type of anther wall development has also been reported in S. nigrum (Saxena and Singh, 1969a), S. nigrum, S. americanum, S. luteum, S. nodiflorum, S. sarache-

idea and *S. villosum* (Saxena and Singh, 1969b) and *S. trigonum* (Ahmad and Siddiqui, 1981). Basic type of anther wall development as recorded in *S. khasianum* is the first record in the genus. However, Basic type of anther wall development has been reported earlier in *Withania somnifera* (See, Davis, 1966) and *Nicandra physaloides* (Prasad and Singh, 1978). On the basis of diagrams of Mohan Ram and Kamini (1964), the development of anther wall layers in *Withania somnifera* appears to follow Dicotyledonous type. On the contrary Monocotyledonous type of anther wall development has been reported in *Nicotiana* (Jos and Singh, 1968).

Davis (1966) considered that Dicotyledonous and Monocotyledonous types of anther wall development have evolved from Basic type by suppression of periclinal division in the outer or inner secondary parietal layer. The reduced type is most advance where periclinal division in both the secondary parietal layers is suppressed. However, it may be concluded that *S. khasianum* occupies a primitive position, while *S. aethiopicum*, *S. citrullifolium*, *S. integrifolium* and *S. sisymbrifolium* an advance position in the family Solanaceae.

The epidermis is thin walled and single layered. Multilayered endothecium as observed in *S. aethiopicum*, *S. citrullifolium*, *S. integrifolium*, *S. khasianum* and *S. sisymbrifolium* has also been reported in *Nicotiana tabacum* and *N. glutinosa* (Jos and Singh, 1968), *Nicandra physaloides* (Prasad

and Singh, 1978) and Solanum triquetrum (Ahmad and Siddiqui, 1981). On the other hand single layered endothecium has been reported in Lycium europaeum (Jain, 1956) and S. nigrum (Saxena and Singh, 1969a). The endothecium develops fibrous thickenings except in genera with porous dehiscene (See, Davis, 1966). Eames (1961) while commenting on the fibrous endothecium has remarked "Forms transitional to longitudinal dehiscence have some fibrous tissue, restricted usually to areas around the pore-Solanaceae". He (1961) also reported that association of poricidal dehiscence and a fibrous layer, through out the length of pollen sac is rare. However, fibrous thickenings usually develop at the tip region in S. aethiopicum, S. citrullifolium, S. integrifolium, S. khasianum and S. sisymbrifolium as reported earlier in S. nigrum, S. americanum, S. luteum, S. nodiflorum, S. sarachoides and S. villosum (Saxena and Singh, 1969b). On the other hand in S. tuberosum (Young, 1923), Lycium europaeum (Jain, 1956), S. macranthum (Mohan, 1970) and S. triquetrum (Ahmad and Siddiqui, 1981) the endothecium is completely devoid of fibrous thickenings. However, in Withania somnifera (Mohan Ram and Kamini, 1964) the endothecium becomes fibrous.

Middle layers are ephemeral and degenerate during the pollen maturity as reported in other species of Solanaceae. Tapetum is of dual origin. It is single layered in the species described here. Occasional occurrence of 2-layered tapetum at

places in S. sisymbrifolium has not been reported elsewhere in the family Solanaceae. Glandular tapetum as described in the present materials is a characteristic feature of the family Solanaceae (Smith, 1935; Cochran, 1938; Jain, 1956; Mohan Ram and Kamini, 1964; Jos and Singh, 1968). However, O'Neil (1920) has reported secretory, amoeboid and persistent types of tapetum in Datura stramonium. Multinucleate tapetal cells as described in the present materials have also been reported earlier in Lycopersicum esculentum (Brown, 1949), Solanum nigrum and S. dulcamara (Turala and Norytkiewicz, 1964), S. nigrum (Saxena and Singh, 1969a) and S. triquetrum (Ahmad and Siddiqui, 1981). Occurrence of Ubish granules in the tapetal cells of S. sisymbrifolium is the first record in the genus and have been reported in Nicandra physaloides (Prasad and Singh, 1978).

Namikawa (1919) for the first time described resorption tissue in the anthers of Solanaceae, but most of the subsequent workers (Young, 1923; Smith, 1935; Cochran, 1938; Barnard, 1949; Jain, 1956; Avery et al., 1959; Mohan Ram and Kamini, 1964; Jos and Singh, 1968) failed to observe it. It has now been described in large number of plants of the family (Singh and Saxena, 1968; Saxena and Singh 1969a,b). The author has also observed resorption tissue in S. aethiopicum and S. citrullifolium. Resorption tissue is hypodermal in origin. In Solanaceae the epidermis does not contribute to the

resorption tissue Senau stricta as described in Ericaceae (Matthews and Knox, 1926; Ganapathy and Palser, 1964) and Leguminoseae (Venkatesh, 1956a, 1956b, 1957).

The number, nature and organization of cells forming resorption tissue vary in different species. The manner of lysis and the formation of resorption cavity and resorption passage between the pollen sacs of an anther lobes clearly demonstrate the primary function of this tissue. It is to bring about confluence between the microsporangia of an anther lobe and to facilitate anther dehiscence (See Singh and Saxena, 1968; Saxena and Singh, 1969a,b). The longitudinal dehiscence of anther of Solanaceae is the result of disjuction of cells forming stomium and not their disintegration.

Atropoeus (1903) has suggested that the lysis of resorption tissue is due to the enzyme action, but Namikawa (1919) and Matthews & Knox (1926) attribute it to the action of oxalic acid and correlate the presence of calcium oxalate crystals in the cells of the connective with granular material occurring in the cells of resorption tissue which they regard of the same nature. According to Eames (1961) "poricidal dehiscence has apparently been derived independently in different taxa from longitudinal dehiscence by shortening the slit. Thus S. integrifolium, S. khasianum and S. sisymbrifolium, are advance where the dehiscence is strictly porous as recorded in majority of the Solanaceae.

On the other hand

the dehiscence of anther by means of apical pore as well as by small pores formed at regular intervals on longitudinal suture in S. aethiopicum and S. citrullifolium has not been recorded earlier in the family Solanaceae and appears to be intermediate.

The male archesporium is hypodermal in origin and is uniseriate in S. aethiopicum, S. citrullifolium, S. integrifolium, S. khasianum and S. sisymbrifolium as recorded earlier in Lycopersicum (Smith, 1935), Capsicum (Cochran, 1938), Lycium europaeum (Jain, 1956), Datura (Avery et al., 1959), Withania somnifera (Mohan Ram and Kamini, 1964), Nicotiana (Jos and Singh, 1968) and Solanum nigrum (Saxena and Singh, 1969a). On the other hand Young (1923) has reported a 2-layered horse-shoe-shaped male archesporium in Solanum tuberosum. A careful examination of Young's figure-2 in support of his observation shows transection of a well developed anther with differentiated wall layers and a 2-layered horse-shoe-shaped sporogeneous tissue. The latter was mistaken by him for the male archesporium.

The number of sporogenous layers in transection is fairly constant and a great similarity exists in microsporogenesis and development of male gametophyte. Chromosomal abnormalities at meiosis I and II have also been observed in natural population of S. citrullifolium, S. integrifolium, S. khasianum and S. sisymbrifolium which have not been recorded

earlier in the family Solanaceae except laggards in S. triquetrum (Ahmad and Siddiqui, 1981). The microspore tetrads are generally tetrahedral in the described Solanaceae.

Occasional occurrence of decussate and rarely isobilateral microspore tetrads in the present materials has been described earlier in Withania somnifera (Mohan Ram and Kamini, 1964), Solanum nigrum, S. americanum, S. nodiflorum, S. luteum, S. sarachoides and S. villosum (Saxena and Singh, 1969b) and S. triquetrum (Ahmad and Siddiqui, 1981). Rare occurrence of rhomboidal microspore tetrad in S. khasianum and S. sisymbrifolium has only been reported in S. triquetrum (Ahmad and Siddiqui, 1981). However, Khan (1951) has reported linear microspore tetrad in S. tuberosum.

The pollen grains are shed at 2-nucleate stage in S. citrullifolium, S. khasianum and S. sisymbrifolium as recorded earlier in Lycium europaeum (Jain, 1956), Withania somnifera (Mohan Ram and Kamini, 1964), Nicotiana (Jos and Singh, 1968), S. nigrum (Saxena and Singh, 1969a), S. nigrum, S. americanum, S. nodiflorum, S. luteum, S. sarachoides and S. villosum (Saxena and Singh, 1969b) and Nicandra physaloides (Prasad and Singh, 1978), while in S. aethiopicum and S. integrifolium the pollen grains are shed at 3-nucleate stage as reported in Nicotiana (Podubnaja-Arnoldi, 1936), Capsicum frutescens Var. Japanese variegated (Lengel, 1960) and S. triquetrum (Ahmad and Siddiqui, 1981). On the other hand

Barnard (1949) reports the degeneration of vegetative nucleus before the shedding in Duboisia leichhardtii and D. myoporoides. The pollen grains are shed at secondary one celled stage.

The pollen grains are tricolporate with smooth exine in the present materials as reported in Lycium europaeum (Jain, 1956), Withania somnifera (Mohan Ram and Kamini, 1964), Solanum nigrum, S. americanum, S. luteum, S. nodiflorum, S. sarachoides and S. villosum (Saxena and Singh, 1969b) and S. trigonum (Ahmad and Siddiqui, 1981). Occasional occurrence of multicolporate pollen grains as described in S. integrifolium has been reported in the family Solanaceae (See Varghese, 1967).

The germination of pollen grain is monosiphonous. Polysiphonous condition and in situ germination of pollen grains as observed in S. citrullifolium have been reported in Lycium europaeum (Jain, 1956) and Withania somnifera (Mohan Ram and Kamini, 1964).

The ovules in Solanaceae are interpreted variously. The ovules are anatropous, unitegmic and tenuinucellate in *S. aethiopicum*, *S. citrullifolium*, *S. integrifolium*, *S. khasianum*, and *S. sisymbrifolium* as recorded in *Nicotiana rustica*, *N. tabacum* and *Datura stramonium* (Chatin, 1874), *Lycopersicum esculentum* (Cooper, 1931; Smith, 1935), *Solanum melongena* (Bhaduri, 1932), *Nicotiana plumbaginifolia*, *Petunia nyctaginiflora* (Bhaduri, 1935), *Capsicum frutescens* Var. grossus (Cochran, 1938), *Lycium europaeum* (Jain, 1956), *Capsicum frutescens* Var. Japanese variegated ornamental (Lengel, 1960), *Browallia demissa* (Mohan, 1966), *Nicotiana tabacum*, *N. rustica*, *N. glutinosa*, *N. glauca*, *N. megalosiphon*, *N. trigonophylla*, *N. longiflora* and *N. alata* (Jos and Singh, 1968), whereas the ovules are half anatropous in *Brunfelsia americana*, *Datura fastuosa*, *Lycopersicum esculentum*, *Physalis minima*, *P. peruviana*, *Withania somnifera* (Bhaduri, 1935) and anacampylotropous in *Solanum nigrum* (Saxena and Singh, 1969a), *S. nigrum*, *S. americanum*, *S. nodiflorum*, *S. luteum*, *S. sarachoides* and *S. villosum* (Saxena and Singh, 1969b), *S. macranthum* (Mohan, 1970) and *Nicandra physaloides* (Prasad and Singh, 1978). Both anatropous and campylotropous ovules are recorded in *Datura* (Avery *et al.*, 1939) and *Solanum pharnaceum* (Dnyansagar and Cooper, 1960), campylotropous and amphitropous ovules have been described in *Cestrum diurnum* and *C. nocturnum* (Bhaduri, 1935) and *Solanum tuberosum* (Rees-Leonard, 1938). Occurrence of orthotropous ovules as in *S. khasianum* has not been reported in the family Solanaceae. Innermost layer of integument differentiates as

endothelium,a characteristic feature of the Solanaceae. According to Eames (1961) the reduction of the integument to one by union of two or less of inner one and of nucellus to a single layer of cells above the sporogenous tissue is common in more specialized families.

Thus the occurrence of unitegmic and tenuinucellate ovules in the present materials may be regarded as an advance character than the bitegmic ovules with massive nucellus.

As observed in the present materials, the female archesporium is generally single celled in Solanaceae (Cooper, 1931; Bhaduri, 1935; Smith, 1935; Cochran, 1938; Jain, 1956; Lengel, 1960; Mohan Ram and Kamini, 1964; Jos and Singh, 1968; Saxena and Singh, 1969a; Prasad and Singh, 1978 and Ahmad and Siddiqui, 1981). Occasional occurrence of multicelled archesporium in S. aethiopicum, S. citrullifolium, S. integrifolium, S. khasianum and S. sisymbrifolium has also been reported earlier in S. melongena (Bhaduri, 1932), Lycopersicum esculentum, Physalis peruviana, Salpiglossis sinuata, Nicotiana plumbaginifolia and Brunfelsia americana (Bhaduri, 1935), S. tuberosum (Rees-Leonard, 1938), Datura species (Gliščić, 1928; Avery et al. 1939), S. nigrum, S. americanum, S. luteum, S. nodiflorum, S. xanthoides and S. villosum (Saxena and Singh, 1969b), S. macranthum (Mohan, 1970), Nicandra physaloides (Prasad and Singh, 1978) and S. trilobatum (Ahmad and Siddiqui, 1981).

Occurrence of accessory archesporium in the present materials has not been reported in the genus Solanum. However, Varghese (1967) has recorded the presence of accessory cells in Solanaceae. Megaspore tetrads are generally linear and the embryo sac usually develops from the chalazal megaspore in the family Solanaceae (Ferguson, 1927; Bhaduri, 1932; Rees-Leonard, 1935; Williams, 1955; Mohan Ram and Kamini, 1964; Saxena and Singh, 1969a,b; Mohan , 1970; Ariz et al., 1972; Ahmad and Siddiqui, 1981). Occasional occurrence of T-shaped megaspore tetrads in S. aethiopicum, S. citrullifolium, S. integrifolium and S. sisymbrifolium and inverted T-shaped in S. aethiopicum and S. citrullifolium has not been recorded in the family. Variations in the number and position of healthy megaspores as observed in present materials have also not been recorded elsewhere in the family Solanaceae.

Monosporic Polygonum type of female gametophyte development as described here has been reported earlier in Centrum splendense and Nicotiana tabacum (Guignard, 1982), Atropa belladona (Souèges, 1907), Nicotiana (Palm, 1922), Datitabac and Hyoscyamus niger (Svensson, 1926), Lycopersicum esculentum (Banerji, 1931), Solanum melongena (Bhaduri, 1932), Nicotiana rustica (Persidsky and Modilewski , 1935), Duboisia hopwoodii and D. myoporoides (Barnard, 1949), Lycium europaeum (Jain, 1956), Withania somnifera (Mohan Ram and Kamini, 1964), Ariz et al., 1972), Nicotiana tabacum, N. rustica N. plumbaginifolia, N. longiflora, N. alata (Jee and Singh,1968),

S. nigrum (Saxena and Singh, 1969a), S. nigrum, S. americanum, S. luteum, S. nodiflorum, S. sarachoides and S. villosum (Saxena and Singh, 1969b), S. macranthum (Mohan, 1970) and S. triquetrum (Ahmad and Siddiqui, 1981).

On the contrary Nanetti (1912) in S. muricatum and Young (1923) in S. tuberosum observed tetrasporic Adoxa type of female gametophyte development. Bhaduri (1932) criticized the observations of Nanetti (1912) and Young (1923) and recorded Polygonum type of female gametophyte development in S. melongena and S. nigrum. Later, Bhaduri (1935) emphasized that Polygonum type of female gametophyte development is a common feature in the genus Solanum. Modilewski (1935) described "Scilla" type of embryo sac in Nicotiana glauca but Jos and Singh (1968) have shown that it follows Polygonum type not only in N. glauca but in seven other species of the genus.

Twin embryo sacs at various stages of development as recorded in S. aethiopicum, S. citrullifolium, S. integrifolium, S. khasianum and S. sisymbrifolium have been reported in Solanum tuberosum (Young, 1922), S. melongena (Bhaduri, 1932), Withania somnifera and Physalis minima (Banerji and Bhaduri, 1933), S. nigrum, S. americanum, S. luteum, S. nodiflorum, S. sarachoides and S. villosum (Saxena and Singh, 1969b).

Monosporic Polygonum type of female gametophyte development as described in the present materials is considered to be the most primitive from which bisporic (Allium and Endymion)

type can be derived by the absence of cell plate formation after meiosis II and suppression of one mitotic division during gametogenesis; similarly if there is no cell plate formation after meiosis I and II and only a single mitotic division occurs, this results in a Tetrasporic Adoxa type of development.

However, the development of female gametophyte is monosporic with a tendency towards bisporic in Lycopersicum esculentum (Cooper, 1931), Nicotiana glauca (Modilewski,1935), Withania somnifera (Mohan Ram and Kamini, 1964), Cestrum elegans, Capsicum frutescens, Nicotiana rustica (See Davis, 1966) and tetrasporic in S. muricatum (Nanetti, 1912) and S. tuberosum (Young, 1923). Thus the above mentioned species may be considered under evolution.

Pollination is anemophillous. The entry of the pollen tube into the ovule is porogamous in Solanaceae (Dnyansagar and Cooper, 1960; Saxena and Singh, 1969a,b; Mohan,1970; Prasad and Singh, 1978) as described in the present investigation. Formation of secondary nucleus before the entry of pollen tube as observed here has also been reported in Petunia (Cooper, 1931), Solanum dhurgia (Dnyansagar and Cooper, 1960) and S. trigonatrum (Ahmad and Siddiqui, 1981).

On the other hand Ferguson (1927) described that in Petunia nyctaginiflora secondary nucleus divides before fertilization and the second male gamete fuses with the nucleus of

the micropylar cell. According to her (1927) one fourth of the growing endosperm derived from the micropylar cell is triploid and that from the chalazal cell is diploid. However, Cooper (1946) re-investigated two varieties Elk's Pride and Topaz queen and reported that double fertilization takes place in usual manner and the entire endosperm is triploid.

The development of endosperm in Solanaceae is Nuclear, Cellular and Helobial (Davis, 1966). The endosperm development in S. aethiopicum, S. citrullifolium, S. integrifolium, S. khasianum and S. sisymbrifolium is ab initio Cellular as reported earlier in Atropa, Datura, Physochlaena, Salpiglossis variabilis and Scopolia (Dahlgren, 1923), Petunia (Cooper, 1946), Solanum phureja (Dnyansagar and Cooper, 1960), Lycium europaeum (Jain, 1962), Withania somnifera (Mohan Ram and Kamini, 1964), Nicotiana (Jos and Singh, 1968), Solanum nigrum (Saxena and Singh, 1969a), Solanum nigrum, S. americanum, S. luteum, S. nodiflorum, S. sarrachoides and S. villosum(Saxena and Singh, 1969b), S. macranthum (Mohan, 1970) and Nicandra physaloides (Prasad and Singh, 1978). Nuclear type of endosperm has been reported in Hyoscyamus orientalis, Salpiglossis and Scopolia atropoides (Hofmeister, 1858), Schizanthus pinnatus (Samuelsson,1913; Dahlgren, 1923), Lycium barbarum (Poreidsky, 1935), Capsicum frutescens Var. grossus (Cochran, 1938) and Solanum trigynum (Ahmad and Siddiqui, 1981). On the other hand Svensson (1926) has described Cellular as well as Helobial types of endosperm development in Hyoscyamus niger in which the

micropylar chamber is small and chalazal one large. The early divisions in the chalazal chamber are always free nuclear forming 26-30 nuclei. Variations in the type of divisions in micropylar chamber have been observed. The divisions may be free nuclear or each division may be followed by wall formation or the first division is by a vertical wall followed by free nuclear divisions. The second condition is more frequent than the first and third types. In H. niger (Svensson, 1926) most of the endosperm is produced by large chalazal chamber. Barnard (1949) also feels that probably the development of endosperm is Helobial in Duboisia leichhardtii and D. myoporoides. According to him (1949) the primary endosperm nucleus migrates to the chalazal end where it divides many times before the division of zygote. Several densely cytoplasmic cells settle down at the bottom of the sac and form a base upon which a free nuclear endosperm is formed.

The first division in the primary endosperm cell is transverse in the present materials as reported earlier in Datura laevis (Guignard, 1902), Petunia nyctaginifolia (Cooper, 1946), Withania somnifera (Mohan Ram and Kamini, 1964), Nicotiana tabacum (Jee and Singh, 1968), Solanum macranthum (Mohan, 1970) and Nicandra physaloides (Prasad and Singh, 1978) while the first division is longitudinal in Petunia nyctaginiflora, Lycopersicum esculentum (Bhaduri, 1933), S. phureja (Dnyansagar and Cooper, 1960) and Solanum macranthum (Mohan, 1970). The second division in both the primary endosperm

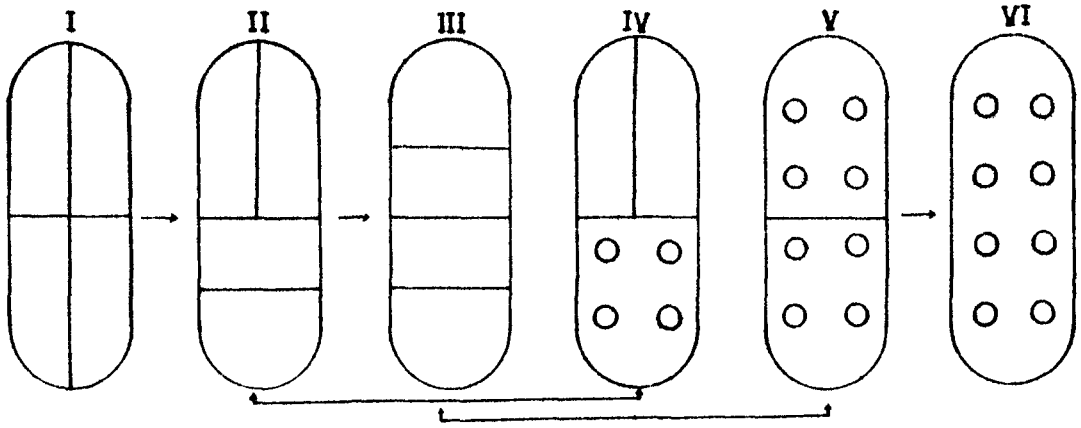
chambers is longitudinal in S. aethiopicum, S. citrullifolium, S. khasianum and S. sisymbrifolium and occasionally in S. integrifolium, whereas in S. macranthum (Mohan, 1970) and Nicandra physaloides (Prasad and Singh, 1978) the division in both the primary endosperm chambers in transverse.

T-shaped arrangement of four cells of endosperm as described in S. integrifolium and occasionally in S. aethiopicum, S. citrullifolium and S. khasianum and occasional occurrence of inverted T-shaped arrangement as recorded in S. integrifolium, S. khasianum and S. sisymbrifolium have not been reported earlier in the family Solanaceae.

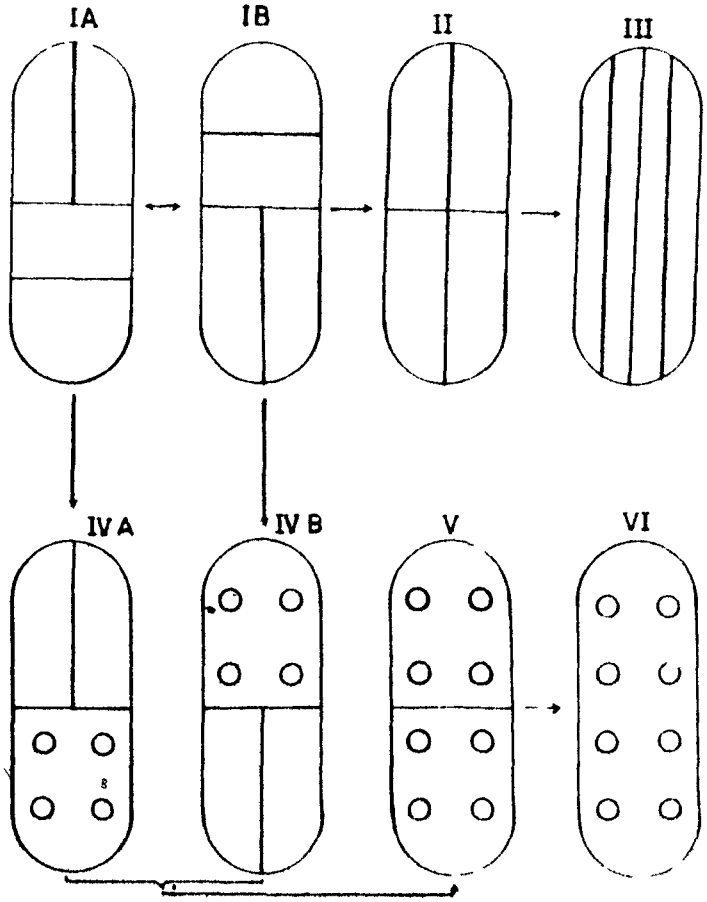
Rosen (1947) while commenting upon the endosperm in Tubiflorae, recognizes six types of endosperm in Solanaceae. His types I-VI are presented in the figure which also give their relationships. Rosen (1947) regards Cellular endosperm to be the most primitive type and the Helobial and Nuclear derived from it. Cellular is the common type of endosperm in the family, whereas the other types are rare and in some cases need confirmation. Among the Cellular types, Rosen believes that his type I is the most primitive and compared it with the "Verbascum" type of Scrophulariaceae. Type-I is characterized by vertical division in both the chambers of 2-celled endosperm. However, the occurrence of transverse division in 2-celled endosperm in Nicandra physaloides which fits in well under the type III of Rosen (1947) deserve careful consideration in any

assessment of phylogenetic relationship of endosperm in this family. Nicandra belonging to the tribe Nicandreae occupies a primitive position in modern classification of the family Wettstein, 1935). It also shows many primitive features in its morphology and life history namely, trifurcate stamen supply, 5-carpellary and 5-1 locular ovary, thin placenta, persistent pollen tube, thin walled persistent endothelium and a number of hypodermal layers persisting in seed coat. These facts and a recent critical discussion on endosperm in Veronica by Tiagi (1966) who regards the endosperm development of Veronica longiflora in which transverse division takes place in the micropylar chamber at the second cell generation, as primitive, has led the present author to believe that type III of Rosen (1947) represents the most primitive condition of endosperm in Solanaceae. It may be pointed out that the Rosen's type IV and V are only known as abnormalities in Hyoscyamus niger (Svensson, 1926). These have not been considered by any worker so far.

However, I am convinced with the scheme of Rosen (1947) showing the evolution of endosperm in Solanaceae. Considering the Rosen's (1947) assumption that Nuclear type of endosperm has been derived from the Cellular type, I have also presented a scheme which differs from Rosen's (1947) scheme. The present scheme is totally based upon the assumption that the transverse division in the primary endosperm chambers is primitive and longitudinal division in both the endosperm chambers



ROSEN (1947)



AUTHOR'S VIEW

DIAGRAMMATIC REPRESENTATION OF THE PROBABLE EVOLUTIONARY SEQUENCE OF THE ENDOSPERM TYPES IN SOLANACEAE

as advance. In the authors scheme S. sisymbrifolium occupies an advance position where the endosperm development follows type II and occasionally III. In S. integrifolium the endosperm follows type IA and occasionally type IB and type II and thus has been considered primitive among the species studied by the author. On the other hand in S. aethiopicum, S. citrullifolium and S. khasianum, the endosperm development follows type II and occasionally type IA and even IB and occupy intermediate position. The types IVA and IVB are considered to be derived from IA and IB respectively from which type V and VI have been derived.

Nicotiana variation of Solanad type of embryogeny as described in S. citrullifolium, S. khasianum and S. sisymbrifolium and occasionally in S. integrifolium has been recorded earlier in S. tuberosum, Datura stramonium, Physalis edulis and Atropa belladona (Tognini, 1900), Nicotiana, Hyoscyamus, Datura, Atropa (Souèges, 1920a,b; 1922), Nicotiana rustica (Pereidsky and Modilewski 1935; Modilewski, 1937), Physalis minima, Withania somnifera and Petunia nyctaginiflora (Bhaduri, 1936), Schizanthus and Petunia (Souèges, 1936), Physalis peruviana (Crété, 1954), Solanum denisaum (Walker, 1955), Saracha jaltomata (Crété, 1960), Solanum pharaia (Dnyansagar and Cooper, 1960), Datura tatula (Crété, 1961a), Browallia demissa (Crété, 1961b), Solanum nigrum, S. americanum, S. luteum, S. nodiflorum, S. sarrachoides and S. villosum (Saxena and Singh, 1969b) and S. trilobatum (Ahmad and Siddiqui, 1981). Occurrence of Myoscetis

variation of Chenopodiad type of embryogeny as described in S. aethiopicum, S. integrifolium and rarely in S. citrullifolium and S. sisymbrifolium has not been recorded so far in the family Solanaceae. Rare occurrence of Onagrad type of embryogeny in S. aethiopicum and S. integrifolium has been recorded as normal feature in Capsicum annuum (Crété, 1961c).

The occurrence of adventive embryos from the cells of endothelium in S. citrullifolium has been recorded earlier in S. macranthum (Mohan, 1970). Adventive embryony has also been recorded in Petunia nyctaginiflora, Withania somnifera and Nicotiana plumbaginifolia (Banerji and Bhaduri, 1933) and N. tabacum (Jos and Singh, 1968). These authors considered the additional embryos to be of nucellar origin. Recent studies on the development of ovule and seed in Solanaceae by Saxena and Singh (1969a,b), Prasad and Singh (1978) and Ahmad and Siddiqui (1981) and the present study clearly show that the nucellus is completely absorbed at 2-nucleate embryo sac stage. Thus there is no trace of nucellus in fertilized ovule and accordingly nucellar origin of accessory embryos appears to be incorrect. Cooper (1943) on the basis of haploid seedlings in interspecific hybridization in Nicotiana regards the accessory embryos of synergid origin. Cameron (1949) has also observed cases of polyembryony in Nicotiana tabacum with seedlings having different chromosome number.

Cleavage of young preembrye as observed in S. integrifolium has been recorded earlier in Nicotiana tabacum (Cooper, 1931), where he observed that additional embrye had apparently arisen as an outgrowth from the apex of the primary embrye.

According to Eames (1961) presence of a long suspensor is a primitive character. Thus S. khasianum having longest suspensor in the described species and may be treated as most primitive species in the family Solanaceae.

The ontogeny and structure of seed in the present investigation broadly resemble that of other species of Solanaceae (Soueges, 1907; Netolitzky, 1926; Dnyansagar and Cooper, 1960; Saxena and Singh, 1969a,b; Prasad and Singh,1978). Soueges (1907) described the structure and development of seed coat in 146 species belonging to 26 genera including Atropa, Datura, Hyoscyamus, Nicotiana, Scopolia and Solanum. Anatomically the seed comprises seed coat persistent endosperm and mature curved dicotyledenous embrye as observed in the other species of Solanaceae. In S. aethiopicum, S. citrullifolium, S. integrifolium and S. khasianum the seed coat is composed of only epidermis as recorded earlier in Solanum macranthum (Mohan, 1970). On the other hand in S. sisymbrifolium the middle layers of integument degenerate and the seed coat comprises an epidermis and thick walled endothelium as recorded earlier in Solanum nigrum (Dnyansagar and Cooper, 1960), Solanum nigrum, S. americanum, S. luteum, S. sodiflorum, S. xanthocarpum and S.

villosum (Saxena and Singh, 1969b) and thin walled persistent endothelium in S. nigrum (Saxena and Singh, 1969a) and Nicandra physaloides (Prasad and Singh, 1978). However, the degeneration of endothelium has been reported in Nicotiana, Nicandra and Lycium (Soueges, 1907) and S. macranthum (Mohan, 1970).

Epidermis in the mature seed is single layered in the described Solanaceae (Dnyansagar and Cooper, 1960; Saxena and Singh, 1969a,b; Mohan, 1970; Prasad and Singh, 1978) as observed in the present material. Seeds are endospermic. In S. citrullifolium, S. khasianum and S. sisymbrifolium the endosperm extends between the coiled embryo and this part of the endosperm is characterized by a comma head and a slender comma stem as reported earlier in Nicandra physaloides (Prasad and Singh, 1978).

As summarised earlier divergent views have been put forward on the systematic position of the Solanaceae (Engler and Prantl, 1895; Bentham and Hooker, 1873-76; Bessey, 1893; Wettstein, 1935; Gundersen, 1950; Rendle, 1952; Benson, 1957; Porter, 1959; Hutchinson, 1959, 1964; Melchior, 1964; Takhtajan, 1966; Cronquist, 1968).

Majority of the workers recognize close resemblence of Solanaceae with Nolanaceae, Convolvulaceae and Scrophulariaceae. The salient embryological features of Solanaceae are thus compared with these of above families.

Convolvulaceae differs from Solanaceae in having Nuclear endosperm, embryo with massive suspensor and folded cotyledons, seed coat differentiated into four zones and the sub-epidermal origin of the main mechanical layer. Palynologically also Convolvulaceae are different from Solanaceae (Erdtman, 1952). Hence any close affinity between Solanaceae and Convolvulaceae seems to be out of question.

Scrophulariaceae and Nolanaceae show strong affinities with Solanaceae in embryological features. A perusal of literature shows that Scrophulariaceae differs from Solanaceae in Cellular endosperm with well developed micropylar as well as chalazal haustoria and Onagrad type of embryogeny (Banerji, 1961; Tiagi, 1966). In the features of corolla, it compares with tribe Salpiglossideae (Solanaceae) which is regarded to form a link between the two families (Rendle, 1952; Takhtajan, 1966). Absence of micropylar and chalazal haustoria in Mimulus cardinalis and Scrophularia marylandica and Solanad type of embryogeny in Ellisiophyllum pinnatum (See Davis, 1966) are known in Scrophulariaceae. Similarly rudimentary endosperm haustoria have been doubted in Solanum phureja (Dnyansagar and Cooper, 1960). In addition the pollen grains similar to these of Solanaceae occur in Scrophulariaceae (Erdtman, 1952). Though it may be pointed out that embryologically Salpiglossideae is still inadequately investigated, nevertheless, the available data show great plasticity in morphological and embryological

features of the tribe which may well be treated a potential progenitor of Scrophulariaceae.

The Nolanaceae share maximum common features with Solanaceae. Solanaceae differs Nolanaceae mainly in structure of ovary and fruit. The schizocarpic, horny and nutnet-like fruit of Nolanaceae is unlike any Solanaceae but approaches the Boraginaceae. The endosperm development in Nolana is ab initio Cellular but at the second cell generation the division is by vertical walls (Rosen, 1947). The present investigation recognizing the close resemblence and anamolous features of Nolanaceae, favours its origin from Solanaceous stock parallel to Boraginaceae.

Wettstein sub-divided Solanaceae into five tribes; Nicandreae, Solaneae, Datureae, Cestreae and Salpiglossideae. Bentham and Hooker (1873-76) has also grouped the genera of Solanaceae under five sub-orders (tribes) Solaneae, Atropeae, Hyoscymeae, Cestrineae and Salpiglossideae. The former classification is mostly followed by the modern taxonomist (Rendle, 1952; Hutchinson, 1959; Takhtajan, 1966; Willis, 1966). Basak (1967) on the basis of pollen morphology of 93 species belonging to 28 genera of Solanaceae has shown that there are striking differences between the pollen grains of Nicandreae, Solaneae, Datureae, Cestreae and Salpiglossideae. Embryologically Nicandreae, Solaneae, and Datureae form a homogeneous group which differs from Cestreae and salpiglossideae in having anaesmpyle-

trepous ovules, Cellular endosperm, coiled embryo and persistent endothelium. Cestreae and Salpiglossideae on the other hand are characterized by anatropous ovules, Cellular, Helobial or Nuclear endosperm, straight or slightly bent embryo and ephemeral endothelium. Souèges (1907) has described ephemeral endothelium in the genera of Cestreae except Cestrum and Salpiglossideae. The flowers in the former group are always actinomorphic having five fertile stamens whereas in the latter it shows a tendency to zygomorphy and reduction in number of stamen. The flowers in S. citrullifolium are zygomorphic with two types of stamens and thus may be considered as connecting link between the salpiglossideae and Solaneae, though the embryological features are similar. Obviously therefore, embryology seems to point to a polyphyletic origin of Solanaceae as interpreted by Wettstein (1935).

Nicandreae having 3-5 locular ovary, trifurcate staminal supply, Basic type of anther wall development, absence of differentiation of resorption tissue, multicelled female archesporium, Cellular endosperm with transverse division at the second cell generation, multilayered seed coat and thin walled endothelium represent the most primitive tribe of the family. Nicandreae, having monotypic genus Nicandra also stand apart from all other tribes in the structure of pollen grains (Basak, 1967).

Salpiglossideae including genera with strongly Zygomorphic bilipped corolla, reduction in the number of fertile stamen, Nuclear, Helobial and Cellular endosperm and ruminate or non-ruminate coat form an advance tribe in the family.

The comparative embryological features of the species of Solanum investigated here have been given in tabular form which could be helpful in the identification of the species. Evolutionary trends in the genus Solanum itself have also been brought out. Considering the number of species included in the genus Solanum and the paucity of the embryological data it is rather difficult to reach any difinite conclusion. However, it appears that further studies in this interesting group of plants would show a complete sequence of evolution within the genus and the relationships of the latter with other genera of the family.

Thus it may be concluded that the genus Solanum belonging to tribe Solaneae of Solanaceae having approximately 2,000 species shows heteregenity in habit, morphology, embryology, fruit and seed structure. Intensive comparative morphological studies in the broadest sense would yield critical information needed to solve the perplexing problems of classification of this vast genus.

SUMMARY

The morphology and embryology of *S. aethiopicum* L., *S. citrullifolium* A.Br., *S. integrifolium* Lam., *S. khasianum* Clarke and *S. sisymbrifolium* Lam. have been described.

1. The habit, external morphology and floral characters of the above mentioned species have been described.

2. Differentiation of floral parts takes place in acropetal succession.

3. The flowers are pentamerous and actinomorphic in *S. aethiopicum*, *S. integrifolium*, *S. khasianum* and *S. sisymbrifolium*, while pentamerous and zygomorphic in *S. citrullifolium*. Occasionally the flowers may be tetramerous and hexamerous in *S. sisymbrifolium*, hexa and heptamerous in *S. aethiopicum* and *S. integrifolium*. The calyx is persistent and gamosepalous in all the five species. The calyx is accrescent in *S. citrullifolium* and *S. sisymbrifolium*. The corolla is gamopetalous and campanulate in *S. aethiopicum*, *S. integrifolium*, *S. khasianum* and *S. sisymbrifolium*. However, the corolla is zygomorphic in *S. citrullifolium*. Anthers are bithecous and 4-chambered. Heteroanthy is a usual feature in *S. citrullifolium*. One of the anthers is quite large and petaloid. Ovary is bicarpellary, syncarpous, bilocular and superior with swollen axile placenta. Stigma is bilobed in *S. aethiopicum*, *S. citrullifolium*, *S.*

khasianum and S. sisymbrifolium, while 3-lobed in S. integrifolium. Heterostyly is common in S. aethiopicum, S. integrifolium, S. khasianum and S. sisymbrifolium.

4. The anthers are quadrangular in transection. The development of anther wall layers conforms to the Dicotyledoneus type in S. aethiopicum, S. citrullifolium, S. integrifolium and S. sisymbrifolium and Basic type in S. khasianum. Anther wall layers comprise the epidermis, endothecium, middle layers and tapetum. The epidermis is single layered. Endothecium is 1-3 layered in S. aethiopicum, 2-3 layered in S. citrullifolium, S. khasianum and S. sisymbrifolium and 3-4 layered in S. integrifolium. Endothecium is devoid of fibrous thickenings except at the tip region. Middle layers are ephemeral and 1-2 layered in S. aethiopicum and S. citrullifolium, 2-layered in S. integrifolium and S. khasianum and 1-3 layered in S. sisymbrifolium.

Tapetum is of dual origin and is generally single layered in all the five species described here. Occasionally at places it becomes two layered in S. sisymbrifolium. Tapetal cells are 1-2 nucleate in S. aethiopicum, S. khasianum and S. sisymbrifolium, 1-4 nucleate in S. citrullifolium and upto 6-nucleate in S. integrifolium. In S. sisymbrifolium the tapetal cells are filled with Ubish granules.

The wall of the dehisced anther comprises an epidermis and few layers of endothecium. Anther dehisces by apical pore in S. integrifolium, S. khasianum and S. sisymbrifolium, whereas in S. aethiopicum and S. citrullifolium the anthers dehisce by apical pore as well as pores formed at regular intervals on longitudinal suture.

5. The male archesporium is hypodermal in origin and uniseriate. The divisions in all the microspore mother cells of an anther may not be synchronous. Chromosomal abnormalities at meiosis I and II have been observed in S. citrullifolium, S. integrifolium, S. khasianum and S. sisymbrifolium. The microspore tetrads are generally tetrahedral, occasionally decussate. Rarely the tetrads are isobilateral in S. aethiopicum, S. citrullifolium and S. integrifolium and rhomboidal and isobilateral in S. khasianum and S. sisymbrifolium. Rarely one or two microspores in a tetrad may be deformed in S. citrullifolium.

Generally the pollen grains are tricolporate in S. aethiopicum, S. citrullifolium, S. integrifolium, S. khasianum and S. sisymbrifolium. Bicolporate and multicolporate pollen grains have also been observed in S. integrifolium. Variations in the size of nuclei have also been observed in S. citrullifolium, S. integrifolium and S. khasianum.

Pollen grains are shed at 2-nucleate stage in S. citrullifolium, S. khasianum and S. sisymbrifolium, while in

S. aethiopicum and S. integrifolium, they are shed at 2-nucleate stage. Polyziphonous condition and in situ germination of pollen grains are common in S. citrullifolium.

Pollen viability in S. aethiopicum, S. citrullifolium, S. integrifolium, S. khasianum and S. nigrumbrifolium is 24.36%, 66.32%, 87.46%, 92.44% and 39.41% respectively.

The size of the pollen grains measured is 20.45 μ in S. aethiopicum, 21.86 μ in S. citrullifolium, 16.87 μ in S. integrifolium, 22.8 μ in S. khasianum and 19.06 μ in S. nigrumbrifolium.

6. The ovules are anatropous, unitegmic and tenuinucellate in S. aethiopicum, S. citrullifolium, S. integrifolium, S. khasianum and S. nigrumbrifolium and rarely orthotropous in S. khasianum. The endothelium differentiates at 2-nucleate embryo sac stage in S. citrullifolium, S. integrifolium, S. khasianum and S. nigrumbrifolium, whereas in S. aethiopicum it differentiates at functional megaspore stage. The endothelium persists upto maturation of seed in S. nigrumbrifolium, while in other four species it degenerates during the seed development. Hypostase is common in the species described here. It persists upto mature embryo sac stage and degenerates after fertilization.

7. The single celled female archesporium is hypodermal in origin in S. aethiopicum, S. citrullifolium, S. integrifolium, S. khasianum and S. nigrumbrifolium. Occasionally it may be

2-celled in S. citrullifolium, 2-3 celled in S. aethiopicum and S. khasianum and upto 4-celled in S. integrifolium and S. sisymbrifolium. Accessory archesporial cells have also been observed at various stages of megasporogenesis and megagametogenesis in S. aethiopicum, S. citrullifolium, S. integrifolium, S. khasianum and S. sisymbrifolium. Female archesporial cell directly functions as megaspore mother cell. It undergoes meiosis and produces megaspore tetrad. The megaspore tetrads are generally linear in S. aethiopicum, S. citrullifolium, S. integrifolium, S. khasianum and S. sisymbrifolium. Sometimes the megaspore tetrads may be T-shaped in S. aethiopicum, S. integrifolium and S. sisymbrifolium and rarely inverted T-shaped in S. aethiopicum and S. citrullifolium.

The chalazal megaspore remains healthy and rest three degenerate in all the five species described here. Rarely in S. citrullifolium the micropylar megaspore remains healthy and rest three degenerate. Variations in the number and position of healthy megaspores in a tetrad have been observed in S. aethiopicum, S. citrullifolium, S. integrifolium, S. khasianum and S. sisymbrifolium.

8. Development of female gametophyte conforms to monosporic, 8-nucleate and Polygonum type in the present investigation. Egg apparatus consists of two synergids and an egg cell. The polar nuclei fuse forming secondary nucleus prior to the entry of the pollen tube into the embryo sac. The antipodal cells

are ephemeral and degenerate after fertilization. Variations in the number and organization of embryo sac nuclei have been observed in S. aethiopicum, S. citrullifolium, S. integrifolium, S. khasianum and S. sisymbrifolium. Occurrence of twin sacs is a common feature in the species described here.

9. Pollination is anemophillous. Fertilization is porogamous. One synergid is destroyed during the entry of the pollen tube into the embryo sac. The other synergid is also destroyed during the act of fertilization. One male gamete fuses with the egg and the other with the secondary nucleus in S. aethiopicum, S. citrullifolium, S. integrifolium, S. khasianum and S. sisymbrifolium.

10. The development of endosperm is ab initio Cellular. The first division in the primary endosperm cell is transverse forming a primary micropylar and primary chalazal endosperm chambers in S. aethiopicum, S. citrullifolium, S. integrifolium, S. khasianum and S. sisymbrifolium. Occasionally the first division is longitudinal in S. citrullifolium and S. sisymbrifolium. The division in both the primary endosperm chambers is longitudinal forming 4-celled endosperm in S. aethiopicum, S. citrullifolium, S. khasianum and S. sisymbrifolium. In S. integrifolium the primary micropylar endosperm chamber divides longitudinally while primary chalazal chamber transversely forming four cells arranged in a T-shaped manner. The division in both the cells of the micropylar chamber is longitudinal in

S. integrifolium, S. khasianum and S. sisymbrifolium and transverse in S. aethiopicum and S. citrullifolium. The division in two juxtaposed cells of the chalazal endosperm chamber is longitudinal in S. aethiopicum and transverse in S. khasianum and S. sisymbrifolium, whereas in S. citrullifolium a definite sequence is not observed.

The cells of the endosperm in the early stages of development possess vacuolated cytoplasm. At maturity the vacuoles disappear and the cytoplasm becomes rich in reserve food. Cells of mature endosperm develop cellulosic thickenings on their walls in S. aethiopicum and S. khasianum.

11. The zygote divides when sufficient amount of endosperm is formed in S. aethiopicum, S. citrullifolium, S. khasianum and S. sisymbrifolium. While in S. integrifolium the zygote divides when the endosperm is 7-10 celled.

The proembryonic tetrad is linear and the embryogeny conforms to the Myosotis variation of Chenopodiad type in S. aethiopicum and S. integrifolium and Nicotiana variation of Solanad type in S. citrullifolium, S. khasianum and S. sisymbrifolium.

Occasionally the embryogeny conforms to the Myosotis variation of Chenopodiad type in S. citrullifolium and S. sisymbrifolium and Nicotiana variation of Solanad type in S. integrifolium. Rarely the proembryonic tetrad is T-shaped in

S. aethiopicum and S. integrifolium and the embryogeny conforms to the Onagrad type.

Variations in the size and number of cotyledons have also been observed in S. integrifolium. Adventive embryony has been observed in S. citrullifolium. In addition to the zygotic embryos a number of adventive embryos may develop from the cells of endothelium and fill up the embryo sac cavity. In such cases most of the endosperm is consumed which results in the degeneration of zygotic as well as endothelial embryos. The degeneration of zygotic or endothelial embryos may be due to lack of proper nutrition as endosperm does not develop further and is consumed by the endothelial embryos. Thus the resulting seeds are abortive. Cleavage polyembryony has been observed in S. integrifolium.

12. The ontogeny and structure of seed have been described. Anatomically the seed comprises a seed coat, persistent endosperm and mature curveddicotyledoneus embryo. The epidermis is the main protective layer and constitute the seed coat in S. aethiopicum, S. citrullifolium, S. integrifolium and S. khasianum, while in S. nigumbrifolium the seed coat comprises an epidermis and persistent lignified single layered endothelium. The cells of the epidermis develop sclerotic thickenings in the inner portion while the outer regions develop rod-like thickenings.

The cells of persistent endosperm possess starch grains and reserve food material. In S. citrullifolium, S.

khasianum and S. sisymbrifolium the endosperm extends between the coiled embryo and this part of endosperm is characterized by a comma head and a slender comma stem.

The affinities of the Solanaceae with the allied families on the basis of embryological features have been discussed. The evolutionary trends in the genus Solanum itself have been brought out.

LITERATURE CITED

Ahmad, R. and Siddiqui, S.A. 1981. The embryology of Solanum triquetrum Cav.
Jour. Sci. Res. 3:17-20.

Ariz, P., N. Iftikhar and N.R. Khan 1972. The megasporogenesis and development of embryo sac in Withania somnifera.
Pak. Jour. Sci. Ind. Res. 15:196-198.

Artopoeus, A. 1903. Uber den Bau und die Offnungsweise der Antheren und die Entwicklung der Samen der Erikaceen.
Flora 92:309-345.

Augustin, B. 1907. Historisch-Kritische und anatomischentwicklungsges Krichliche Unter-Suchung uber den Paprika.
Thesis, Nemetbogsan.

Avery, A.G., S. Satina and J. Rietsema 1959. 'Blakeslee: The genus Datura.
Ronald Press, New York.

*Banerji, E.A. 1931. Cytology of Capsicum.
M.Sc. Thesis, Calcutta Univ. (unpublished).

Banerji, I. 1961. The endosperm in Scrophulariaceae.
J. Indian bot. Soc. 40:1-11.

Banerji, I. and P.N. Bhaduri 1933. Polyembryony in Solanaceae.
Curr. Sci. 1:310.

Barnard, C. 1949. Microsporogenesis, macrosporogenesis and development of the macrogametophyte and seed of Duboisia leichhardtii and D. myoporoides.
Aust. J. Sci. Res. B. 2:241-248.

Bartling, F.T., 1830. Ordines Naturales Plantarum. Gottingae

Basak, R.K. 1967. The pollen grains of Solanaceae.
Bull. bot. Soc. Bengal 21:49-58.

Benson, L. 1957. 'Plant Classification'.
Heath & Co., Boston.

Bentham, G. and J.D. Hooker 1873-1876. "Genera Plantarum".
London.

Bessey, C.M. 1893. "Evolution and Classification".
Bot. Gaz. 18:329-332.

Bhaduri, P.N. 1932. The development of ovule and embryo sac in Solanum melongena L.
J. Indian bot. Soc. 11:202-224.

Bhaduri, P.N. 1933. A note on the new type of fertilization in plants.
Curr. Sci. 2:95.

Bhaduri, P.N. 1935. Studies on the female gametophyte in Solanaceae.
J. Indian bot. Soc. 14:133-149.

Bhaduri, P.N. 1936. Studies on the embryogeny of the Solanaceae I.
Bot. Gaz. 98:283-295.

Biraghi, D.A. 1929. Impollinazioni tra Nicotiana rustica Var. brasila e Petunia sp. e loro effetti.
Annali di Botanica 18:216-222.

Brown, S.W. 1949. Endomitosis in the tapetum of tomato.
Amer. J. Bot. 36:703-716.

Cameron, D.R. 1949. Inheritance in Nicotiana tabacum XXII. Investigations on multiple seedlings.
Amer. J. Bot. 36:526-528.

Chatin, J. 1874. Etudes sur le developpement de l' ovule et de la graine dans less Scrofularinees, les Solanacees, les Borraginees et les Labiees.
Ann. Sci. Nat. Bot. 19:1-107.

Cochran, H.L. 1938. A morphological study of flower and seed development in pepper.
J. Agric. Res. 56:395-419.

Cooper, D.C. 1931. Macrosporogenesis and development of the macrogametophyte of Lycopersicon esculentum.
Amer. J. Bot. 18:739-748.

Cooper, D.C. 1943. Haploid-diploid twin in Lilium and Nicotiana.
Amer. J. Bot. 30:408-413.

Cooper, D.C. 1946. Double fertilization in Petunia.
Amer. J. Bot. 33:54-57.

Corner, E.J.H. 1976. "The seeds of Dicotyledons".
Vol. I. Cambridge Univ. Press, Cambridge.

Crété, P. 1951. Répartition et intérêt phylogénétique des albumens à formations haustoriales chez les angiosperms et plus particulièrement chez les gamotopétales.
Ann. Sci. Nat. 12:131-191.

Crété, P. 1954. Embryogénie des Solanacées. Les premiers stades du développement de l'embryon chez les Physalis peruviana.
C.R. Acad. Sci. Paris 239:852-854.

Crété, P. 1960. Embryogénie des Solanacées. Développement de l'embryon chez le Saracha jaltomata.
C.R. Acad. Sci. Paris 250:4194-4196.

Crété, P. 1961a. Embryogénie des Solanacées. Développement de l'embryon chez le Datura tatula.
C.R. Acad. Sci. Paris 252:2128-2130.

Crété, P. 1961b. Embryogénie des Solanacées. Développement de l'embryon chez le Browallia demissa.
C.R. Acad. Sci. Paris 252:2921-2923.

Crété, P. 1961c. Embryogénie des Solanacées. Développement de l'embryon chez le Capsicum annuum.
C.R. Acad. Sci. Paris 252:3104-3106.

Crété, P. 1961d. Embryogénie des Solanacées. Développement de l'embryon chez le Salpiglossis sinuata.
C.R. Acad. Sci. Paris 253:3032-3034.

Cronquist, A. 1968. "The evolution and classification of flowering plants".
Thomas Nelson Ltd., London & Edinburgh.

Czaja, A. Th. 1963. Neue untersuchungen an der Testa der Tomatensamen.
Planta (Arch. Wiss. Bot.) 59:262-279.

Czaja, A. Th. 1965. Mikroskopische untersuchungen von Tomatenmark.
Sem. Zeit. Leb. Unt. For. 128:28-32.

Dahlgren, K.V.O. 1923. Notes on the ab initio Cellular endosperm.
Bot. Notiser 1923:1-24.

*Dahlgren, K.V.O. 1939. Sur la presence d'amidon dans Le Sac embryonnaire Chez Les Angiospermes.
Bot. Notiser 1939:221-231.

D'Arcy, W.G. 1976. The classification of the Solanaceae "In the Biology and Taxonomy of the Solanaceae" Ed. J.G. Hawkes, R.N. Lester and A.D. Skelding.
Linn. Soc. Symp. Series 3-47.

Davis, G.L. 1966. "Systematic embryology of the angiosperms".
John Wiley & Sons, New York.

Dnyansagar, V.R. and D.C. Cooper 1960. Development of the seed of Solanum phureja.
Amer. Jour. Bot. 47:176-186.

Eames, A.J. 1961. "Morphology of the angiosperm".
New York.

Engler, A. and K. Prantl 1895. Die naturlichen Pflanzen-familien. Leipzig.

Erdtman, G. 1952. "Pollen morphology and plant taxonomy".
Chronica Botanica, Waltham, Mass. U.S.A.

Ferguson, M.C. 1927. A cytological and a genetical study of Petunia 1.
Bull. Torrey bot. cl. 54:657-664.

Ganapathy, P.S and B.F. Palser 1964. Studies of floral morphology in the Ericales VII. Embryology in the Phyllodoceae.
Bot. Gaz. 125:280-297.

Gbile, Z.O. 1976. Solanum in Nigeria: "In the Biology and Taxonomy of the Solanaceae". Ed. J.G. Hawkes, R.N. Lester and A.D. Skelding.
Linn. Soc. Symp. Series 113-120.

Gbile, Z.O. and M.A. Sowunmi 1976. The pollen morphology of Nigerian Solanum species: "In the Biology and Taxonomy of the Solanaceae". Ed. J.G. Hawkes, R.N. Lester and A.D. Skelding.
Linn. Soc. Symposium series 335-342.

Glišić, L.M. 1928. Zur Entwicklungsgeschichte der Solanaceen. Die Endospermbildung von Datura metel.
Bull. Inst. Jard. Bot. Univ. Belgrade 1:75-85.

Glišić, L.M. 1936-1937. Ein Versuch der Verwertung der Endospermmerkmale fur typologische und phyllogenetische Zwecke innerhalb der Scrophulariaceen.
Bull. Inst. Jard. Bot. Univ. Belgrad 4:42-73.

Goodspeed, T.H. 1947. Maturation of gametes and fertilization in Nicotiana.
Madrano 9:110-120.

Goodspeed, T.H. 1954. "The genus Nicotiana".
Waltham Mass., U.S.A.

Guignard, L. 1882. Recherches sur le sac embryonnaire des Phanérogames angiospermes.
Ann. Sci. Nat. Bot. 6:136-199.

Guignard, L. 1902. La double fecondation chez les Solanees.
Jour. de Bot. 16:145-167.

Gundersen, A. 1950. "Families of Dicotyledons".
Waltham, Mass., U.S.A.

Haberlandt, G. 1931. "Schnarf" Vergleichende Embryologie der angiospermen, 177.

Hofmeister, W. 1858. Neuere Beobachtungen uber die Embryobildung der Phanerogamen.
Jahrb. f. Wiss. Bot. 1:82-190.

Husain, W. 1968. *Solanum trianetrum* Cav. A new record for India from Aligarh (U.P.).
Bull. Bot. Soc. Bengal 22: 237-238.

Hutchinson, J. 1959. "The Families of Flowering Plants".
Vol. I. Dicotyledons. Oxford, Clarendon Press.

Hutchinson, J. 1964. "The Genera of Flowering Plants".
Vol. I. Dicotyledons. Oxford Press.

Jain, T.C. 1956. The gametophytes of *Lycium europaeum* Linn.
J. Indian bot. Soc. 35: 181-188.

Jain, T.C. 1962. Studies in the floral anatomy and embryology of Convolvulaceae, Boraginaceae and Solanaceae.
Ph.D. Thesis, Rajasthan University, Jaipur.

Johansen, D.A. 1950. "Plant Embryology".
Chronica Botanica, Waltham, Mass., U.S.A.

*Jönsson, B. 1881. Ytterligare bidrag till Kannedomen on Angiospermernas embryosackutveckling.
Bot. Notiser 1881: 169-187.

Jos, J.S. and S.P. Singh 1968. Gametophyte development and embryogeny in the genus *Nicotiana*.
J. Indian bot. Soc. 47: 117-128.

Khan, S.I. 1951. Pollen sterility in *Solanum tuberosum* L.
Cytologia 16: 124-130.

Krishna Iyengar, C.V. 1940a. Development of embryo sac and endosperm haustoria in some members of Scrophulariaceae IV. Vandellia hirsuta Ham. and V. asaora Benth.
J. Indian bot. Soc. 18:179-189.

Krishna Iyengar, C.V. 1940b. Development of embryo sac and endosperm haustoria in some member of Scrophularineae V. Ilysanthes hyssopoides Benth. Bonnaya tenuifolia Spreng.
J. Indian bot. Soc. 19:5-17.

Krishnamurty, K.V. and K. Apparao 1958. Abnormal pollen tube development in Nicotiana hybrid.
Curr. Sci. 27:397-398.

Krüger, M. 1932. Vergleichendentwicklungsgeschichtliche untersuchungen an den Fruchtknoten und Fruchten Zweier Solanum Chimaren und ihere Eltermarten.
Platna 17:372-436.

Lengel, P.A. 1960. Development of the pollen and the embryo sac in Capsicum frutescens var. Japanese variegated ornamental.
Ohio J. Sci. 60:8-12.

Lunyeva, M.Z., V.A. Peddubnaja-Arnoldi and N.N. Bhandari 1970. Morphological, cytological and histochemical investigations on Nicotiana alata, N. glauca and their hybrid.
Phytomorphology 20:270-281.

Magtang, M.V. 1936. Floral biology and morphology of the egg plant.
Philippine Agr. 25:30-53.

Matthews, J.R. and E.M. Knox 1926. The comparative morphology of the stamen in the Ericaceae.
Trans. & Proc. bot. Soc. Edinburgh 29:243-281.

Melchior, H. 1964. Solanaceae, 2:444-447. In Engler (Ed.), syllabus der Pflanzenfamilien, 12th Ed. Berlin.

Medilewski, J. 1935. Cytological investigation of the genus Nicotiana. Cytology and embryology of the amphidiploid Nicotiana ditacla.
Vseukr. Akad. Nauk. Inst. Bot. Zhurn. 7:7-29.

Medilewski,J. 1937. Cytological investigation of the genus Nicotiana 3. Cytology and embryology of hybrid N. rustica var. Azerbaidzhan x N. glauca.
Zhur. Inst. bot. Akad. Sci. Ukraine 11:59-71.

Mohan, K. 1966. The ovule and embryo sac development in Browallia demissa Linn.
Proc. Indian Acad. Sci. 64B:26-31.

Mohan, K. 1970. Morphological studies in Solanaceae V. Embryology as well as structure and development of seed of Solanum macranthum Dun.
Agra Univ. J. Res. Sci. 19:53-66.

Mohan Ram, H.Y. and Kamini, I. 1964. Embryology and fruit development in Withania somnifera.
Phytomorphology 14:374-387.

Munting, A.J. 1974. Development of flower and fruit in Capsicum annuum L.
Acta Bot. Neerl. 23:415-432.

Mutafjan, E.M. 1964. Megasporogenesis and formation of the embryo sac in the pepper (Capsicum sp).
IZV. Akad. Nauk. Arm. SSR. Biol. Nauk. 17:93-99.

Nair, P.K.K. 1965. Pollen grains of Western Himalayan Plants. Asbia Pub. House, New Delhi, pp.102.

Namikawa, 1919. Über das offnender antheren bei einigen Solanaceae.
Bot. Mag. (Tokyo) 33:62-69.

Nanetti, A. 1912. Sulla probabili cause della pertenocarpia del Solanum muricatum Ait.
N.G. bot. Ital. N.S. 19:91-111.

Netolitzky, F. 1926. Anatomie der angiospermen Samen.
Berlin.

O'Neal, C.E. 1920. Microsporogenesis in Datura stramonium.
Bull. Torrey bot. cl. 47:231-241.

Palm, P. 1922. Zaadvorming en zaadsteriliteit in Deli-Tabak.
Bull. Deli Proefstation Medan-Sumatra 16.

Peraidsky, D. 1935. On the development of endosperm in Solanaceae.
Zhur. Inst. bot. Akad. Sci. RSS Ukraine 4:35-45.

Peraidsky, D. and J. Modilewski 1935. Cytological and embryological studies of the chief varieties of Nicotiana rustica.
Zhur. Inst. bot. Akad. Sci. RSS Ukraine 3:33-49.

Poddubnaja-Arnoldi, V.A. 1936. Beobachtungen uber die keimung des pollens einiger pflanzen auf kunstlichen Nahrboden.
Planta 25:502-529.

Porter, C.L. 1959. "Taxonomy of Flowering Plants".
Freeman & Co. San Francisco.

Prasad, T. and D. Singh 1970. Gametophytes and seed development in Micandra physaloides Gaertn.
J. Indian bot. Soc. 37:76-83.

Rees-Leonark, O.L. 1935. Macrosporogenesis and development of macrogametophyte of Solanum tuberosum.
Bot. Gaz. 96:734-750.

Rendle, A.D. 1952. "The classification of plants".
Vol. I. Cambridge.

Rosen, W. 1947. The female gametophyte in Nolana and endosperm development in Tubiflorae.
Bot. Notiser 1:372-382.

*Rybchenko, O.I. 1963. Cytoembryological research on the development of the male gametophyte in the Solanaceae.
Ukraine Bot. Zhur. 20:3-14.

*Samuelsson, G. 1913. Studien uber die Entwicklungsgeschichte einiger Bicornes-Typen. Ein Beiträge zur Kenntnis der systematischen Stellung der Diapensiaceen und Empetraceen.
Svensk. bot. Tidskr. 7:97-188.

Saxena, T. and D. Singh 1969a. Embryology and seed development of tetraploid form of Solanum nigrum Linn.
J. Indian bot. Soc. 48:148-157.

Saxena, T. and D. Singh 1969b. Comparative embryology and seed structure of Solanum nigrum complex.
Seminar on Morphology, Anatomy and Embryology of land plants, Department of Botany, Univ. Delhi, 75-78.

Schnarf, K. 1931. Vergleichende Embryologie der Angiospermen. Berlin.

*Schurhoff, P.N. 1926. "Die zytologie der Blutenpflanzen". Stuttgart.

Singh, D. and T. Saxena 1968. Structure, development and dehiscence of anther in Solanaceae. Proc. Indian Sci. Cong. Assoc. III:338-339.

Smith, O. 1935. Pollination and life history studies of the tomato, Lycopersicum esculentum. Cornell Univ. Agr. Exp. Sta. Mem. 184:3-16.

Souèges, R. 1907. Développement et structure du tégument siminal chez les Solanacées. Ann. Sci. Nat. Bot. Ser. 9:1-24. These, Paris.

Souèges, R. 1920a. Embryogénie des Solanacées. Développement de l'embryon chez les Nicotiana. C.R. Acad. Sci. Paris 170:1125-1127.

Souèges, R. 1920b. Embryogénie des Solanacées. Développement de l'embryon chez les Hyoscyamus et Atropa. C.R. Acad. Sci. Paris 170:1279-1281.

Souèges, R. 1922. Recherches Sur l'embryogénie des Solanacées. (Nicotianées; Hyoscyamées; Atropées). Bull. Soc. bot. France 69:163-178, 236-241, 352-365, 385-393.

Souèges, R. 1936. Développement de l'embryon chez le Schizanthus et les Petunias. Bull. Soc. bot. France 83:570-577.

Svensson, H.G. 1926. Zytologische Embryologische Solanaceen Studien I. Über die Samenentwicklung von Hyoscyamus niger L.
Svensk. bot. Tidsky. 20:420-434.

Takhtajan, A.L. 1966. The system and phylogeny of flowering plants.

Tiagi, B. 1966. Development of the seed and fruit in Rhinanthus major and R. serotinus.
Amer. J. Bot. 53:646-651.

Tegnini, F. 1900. Sul l'embriologia di alcune Solanaceae di appunti lasciati.
Atti. Inst. Bot. Pavia 6:109-122.

Turala, K. and K.U. Worythiewicz 1964. Cytological processes during the differentiation of the tapetal layer in Solanum dulcamara and S. nigrum.
Acta Biol. Cracov. Bot. 7:171-183.

Varghese, T.M. 1967. Solanaceae.
Abst. Sem. Comparative Embryology of Angiosperms, Bot. Deptt. Univ. Delhi, p.98.

Vasil, I.K. 1964. Studies on pollen germination of certain Solanaceae.
Bull. Torrey bot. cl. 91:370-377.

Venkatesh, C.S. 1966a. The form, structure and special ways of dehiscence in anthers of Cassia-I, sub-genus Fistula.
Phytomorphology 6:168-176.

Venkatesh, C.S. 1966b. The form, structure and special ways of dehiscence in anthers of Cassia-II, sub-genus Lasiorhegma.
Phytomorphology 6:272-277.

Venkatesh, C.S. 1957. The form, structure and special ways of dehiscence in anthers of Cassia-III, sub-genus Senna. Phytomorphology 7:253-273.

Walker, R.I. 1935. Cytological and embryological studies in Solanum section tuberarium.
Bull. Torrey bot. cl. 82:87-101.

Wangenheim, K.H. Von 1957. Untersuchungen über den zusammenhang Zwischen chromosomenzahl und Kreuzbarkeit bei Solanum Arten.
Z. indukt. Abst. U. Vererb. 88:21-37.

Wettstein, R. Von, 1892. Uber die Systematik der Solanaceen.
Verhandlungen de Zoologisch-Botanishen Gesellschaft in Wien, 42 (Sitzber.):29.

Wettstein, R. 1935. "Handbuch der Systematischen botanik".
Ed. 4th Vienna.

Williams, E.J. 1955. Seed failure in the Chippewa variety of Solanum tuberosum.
Bot. Gaz. 117:10-15.

Willis, J.C. 1966. "A Dictionary of the Flowering plants and Ferns".
Cambridge Univ. Press.

Young, W.J. 1922. Potato ovules with two embryo sacs.
Amer. J. Bot. 9:213-214.

Young, W.J. 1923. The formation and degeneration of germ cells in the potato.
Amer. J. Bot. 10:325-335.

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* Not seen in original.